PARASITIZATION OF *Liriomyza trifolii* (Burgess) BY *Diglyphus intermedius* (Girault)

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1987

ACKNOWLEDGEMENTS

My sincerest thanks to Dr. David J. Schuster, chairman of the supervisory committee for his financial support, guidance and advice.

I express my gratitude for the help given to me by Dr. Savage and Dr. Kerr while they served on the supervisory committee. I am indebted to the late Dr. Sailer who had also served on the supervisory committee and for motivating me in my career.

I would like to thank Dr. Portier and his graduate research assistants for making helpful suggestions for the statistical analysis of the experimental results.

The staff at the Gulf Coast Research Station helped me in many ways while I was at the station doing the experiments. Their help is gratefully acknowledged.

My colleagues and friends provided me with companionship and moral support during my graduate years. Their friendship will always be cherished.

My family provided me with financial and moral support. I am grateful for the help I have received from them.

Finally, my wife Faigani has been patient with me while I was busy with my studies and I wish to thank her for that.

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Abstract of Dissertation Presented to the Graduate
School of the University of Florida in Partial Fulfillment
of the Requirements for the Degree of Doctor of Philosophy

PARASITIZATION OF *Liriomyza trifolii* (Burgess) BY
Diglyphus intermedius (Girault)

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May 1987

Chairman: D. J. Schuster
Major Department: Entomology and Nematology

Diglyphus intermedius (Girault) is a commonly encountered parasitoid of *Liriomyza* species leafminers which are considered important pests of tomato and several other commercially grown crops in Florida. An understanding of the leafminer-parasitoid interactions is important to any sound, integrated pest management system on tomato. Those aspects of the biology of *Diglyphus intermedius* that influence its parasitization of *Liriomyza trifolii* (Burgess), reared on tomato, were determined from laboratory experiments to obtain information on *L. trifolii*-*D. intermedius* interactions.

The relationship between T, temperature in degrees Celsius, and parasitoid fecundity, F, longevity, L, and parasitoid-induced host mortality, Hm, were measured at 15.6, 19.4, 23.3, 27.2, and 31.1 C and are described by the equations: $F = -196.11 + 42.65T - 1.1T^2$ ($r^2 = .65$), $L = 74.32 - 2.09T$ ($r^2 = .94$), and $Hm = 721.97 - 19.1T$ ($r^2 = .83$)

The daily parasitism rate was determined to be a function of leafminer and parasitoid densities and is expressed by the equation: $Y = Kp.a_2.(1 - \exp(-a_1/Kh)$ where Y is the number of hosts parasitized/day, Kp is 7.3908 hosts parasitized/parasitoid-day and Kh is 0.0144 leafminer larvae/sq cm leaf area. Leafminer density, a_1, ranged from 0 to 0.06 larvae/sq cm leaf area. Parasitoid density, a_2, ranged from 1 to 5/cage.

The rate of daily host mortality is described by the equation $Z = Cp.a_2.(1 - \exp(-a_2/Ch))$ where Z is the number of hosts killed/day, Cp is 9.2064 hosts killed/parasitoid-day and Ch is 0.0165 leafminer larvae/sq cm leaf area.

D. intermedius-induced host mortality and parasitization were highest in the first 4 h of a 24 h period, with 12 h of light followed by 12 h of dark. More 120-h-old larvae were parasitized and killed than were 96-h-old larvae when both ages of larvae were equally available to a female parasitoid. An average 0.8, 1.1, 1.35 and 0.98 parasitoid eggs became adults when 1, 2, 3, and 4 eggs were placed on each host larva, respectively.

CHAPTER I
INTRODUCTION

The use of broad-spectrum insecticides on a large scale in the 1940s has led to the emergence of Liriomyza species leafminers as important pests of tomato, chrysanthemum, celery and many other commercial crops grown in Florida (Schuster 1981). The worldwide spread of Liriomyza trifolii (Burgess) in the past decade, in addition, made it an international pest (Poe and Montz 1981a). The balance between leafminers and their natural enemies has presumably been upset by the use of broad-spectrum insecticides under Florida conditions. New or previously unused insecticides have been introduced whenever contemporary ones became ineffective (Leibee 1981b), but these have provided only short term relief. The period of effective use of a newly introduced, broad-spectrum insecticide has usually been followed by loss of control. The exact mechanisms of the breakdown in control are not known.

Damage due to insecticide-induced outbreaks of leafminers can be reduced greatly if the insecticide is selected carefully along with population monitoring and the use of economic thresholds (Waddill 1981). Only recently have host specific insecticides become available for leafminers (Robb and Parrella 1984). Some of these chemicals are still awaiting clearance for commercial use on tomato. (Fluker personal communication 1986). As a result of the failure of long term control of the pest with insecticides, growers have embraced the current philosophy of integrated pest management (IPM) approach (Poe 1985).

Action thresholds have been established for leafminers on tomato in Florida (Pohronezny and Waddill 1978, Schuster et al. 1980). The role that the natural enemies play in determining host population densities has subsequently become crucial to any IPM strategy for leafminer regulation. For example, only live leafminer larvae are counted in determining if leafminers have reached the threshold level that requires insecticide application. The role of natural enemies is recognized and taken into consideration by excluding larvae killed by parasitoids. As a further refinement of IPM tactics, many current research programs are directed toward determining the role of natural enemies in regulating leafminer populations to make IPM programs more robust (Parrella et al. 1985, Schuster 1985, Zehnder and Trumble 1985, and Lindquist and Casey 1985).

Leafminer-parasitoid interaction was a focus of the leafminer population dynamics model for celery proposed by Seerege et al. (1980) and provides an excellent framework for the elucidation of the role of natural enemies in regulating leafminer populations. Their model pertained to within-field populations of eggs, larvae, pupae and adults of leafminers and its parasitoids, broadly expressed as processes that contribute to the overall dynamics of the model. Other processes, such as parasitism, were also incorporated into the model.

One hypothesis about the rate of parasitism is that it is a function of host and parasitoid densities. Holling (1959), for example stated that parasitism rate is directly dependent on host and parasitoid densities. An increase in either density led to higher parasitism rate. This hypothesis motivated Smerage et al. (1980) to utilize the family of curves depicted in Figure 1-1 to illustrate the general relationship between the host and parasitoid densities and the number of hosts parasitized/day. The scale of the family of curves was assumed by Smerage et al. (1980) to fluctuate with temperature.

Musgrave et al. (1980) made some computer simulations of the Smerage et al. (1980) model. Process and parameter descriptions were derived from hypothetical values and preliminary estimates. The results of the simulations were encouraging enough to warrant further research to obtain more complete data to improve the model.

Several workers in Florida are striving for more complete quantitative descriptions of the biologies of leafminers and its parasitoids. This includes research in better estimates of parameters. The ultimate aim of this research is to incorporate a leafminer model into IPM strategies. As results become available, they may be incorporated into the Smerage et al. (1980) model. An alternative model may become necessary if the new information can not be readily incorporated into the existing model without major structural changes.

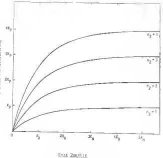

Figure 1-1. Typical functional description of a single host-single parasitoid parasitism (figure obtained from Swerage 1980).

The specific needs being addressed currently are 1) complete quantitative information about the biologies of leafminers and their most common parasitoids and 2) sampling procedures to estimate populations of the leafminers and its major parasitoids. A major thrust of research efforts has been the measurement of fecundity, longevity and development of leafminers and its parasitoids on different crop and weed hosts and at different temperatures. Behavioral phenomena, such as peak periods of ovipositional and feeding activities, have been reported to follow circadian patterns. These are also being studied for the leafminer and its parasitoids.

Another focal point of leafminer research is leafminer-parasitoid interactions. In particular, the extent to which leafminer and parasitoid densities determine the rate of leafminer parasitism is being investigated. Parasitization of a host refers to the act of utilizing a host for oviposition. Parasitoids may also kill hosts without ovipositing on them. Therefore, the effect of host and parasitoid density on the rate of parasitoid-induced host mortality is also being investigated. The term parasitoid-induced host mortality is from hereon used to refer to the sum of hosts killed by parasitoids for ovipositional and non-ovipositional purposes. In other words, it is the number of successful attacks by parasitoids that lead to death of hosts.

More than one egg of a parasitoid may be deposited when a host is parasitized. Multiple oviposition may lead to reduced survivorship of the progeny of parasitoids. In addition, not all host larvae may be equally acceptable to parasitoids for ovipositional or non-ovipositional purposes. Therefore, there are current investigations of multiple oviposition and parasitoid preference for a particular size of leafminer larvae.

The objectives of the research presented here were

1) To determine the rates of parasitism and parasitoid-induced host mortality as functions of leafminer and parasitoid densities, with temperature being kept constant

2) To determine the effect of temperature on parasitoid fecundity, female parasitoid longevity and parasitoid-induced host mortality.

3) To determine the role of time of day on parasitoid oviposition and parasitoid-induced host mortality rates during different times within a day.

4) To determine the influence of host age on parasitoid oviposition and parasitoid-induced host mortality.

5) To determine the influence of multiple oviposition by the parasitoid on the survivorship of the parasitoid progeny.

In the Smerage et al. model (1980), all parasitoid species were aggregated into a single equivalent parasitoid population to simplify the model. There are many parasitoids that attack *Liriomyza trifolii*, however. In addition, the biologies of these different species vary. For the research presented here it was possible to investigate only one parasitoid species, *Diglyphus intermedius* (Girault), with the resources and time available.

D. intermedius was chosen as a representative natural enemy of the leafminers for two reasons. *D. intermedius* is one of the three most common parasitoids reared from leafminers on tomato in Florida (the other two are *Chrysonotomyia* sp. (Eulophidae) and *Opius* sp. (Braconidae)) (Schuster 1985). *D. intermedius* is an ectoparasitoid, laying its eggs on or near the host larva (Hendrickson and Barth 1978). This makes *D. intermedius* easier to observe than either *Chrysonotomyia* sp. or *Opius* sp., which are endoparasitoids (Lema 1976).

Before initiating any experimental work, the literature on leafminer and *D. intermedius* was reviewed (see Chapter II). To study the biology of the parasitoid and its interaction with leafminers, experiments should ideally be done in the field. It is not possible to vary a single factor and keep all others constant in the field, however. All experiments were, therefore, done in the laboratory. *L. trifolii* and *D. intermedius* were initially collected from tomato fields and subsequently reared on tomato in controlled environmental conditions to ensure an adequate supply for use in the experiments. The insect rearing techniques are described in Chapter III.

The first series of replicated experiments determined the influence of temperature on *D. intermedius* fecundity, longevity and _D. intermedius_-induced host mortality (Chapter IV). Hendrickson and Barth (1978) had shown that _D. intermedius_ usually oviposited on 3rd-instar hosts although it killed all three instars. Leafminer larvae in their 3rd-instar were kept in petri dishes and placed in 5 incubators each set at a different constant temperature in the 15.6 to 31.1 C range. A pair of parasitoids was introduced into each petri dish. Killed hosts and parasitized hosts were counted daily. Leafminer larvae from the previous day were replaced with more 3rd-instar larvae. The petri plates were maintained until the female parasitoids died.

In the temperature range studied, the temperature dependence of F, the average fecundity per adult female lifespan, was described by the equation:

$$F = -196.11 + 42.65T - 1.1T^2 \quad (r^2 = .65) \qquad (1)$$

When the number of hosts was a non-limiting resource, the temperature dependence of Bm, the average number of hosts killed/adult female lifespan, was described by the equation:

$$Bm = 721.97 - 19.1T \quad (r^2 = .83) \qquad (2)$$

Finally, the temperature dependence of L, the average female parasitoid longevity in days, was described by the equation.

$$L = 74.32 - 2.09T \quad (r^2 = .94) \qquad (3)$$

In these and all subsequent equations, T denotes temperature in degrees Celsius. As a female parasitoid aged, daily parasitism and parasitoid-induced host mortality rates declined. Temperature determined the adult female parasitoid age at which oviposition and parasitoid-induced host mortality rates peak. With an increase in temperature, these peaks are reached earlier.

Experiments to determine the effect of time of day on parasitoid-induced host mortality and parasitization were done in a controlled environment room (Chapter V). The room was maintained at 25-27 C. Fluorescent lighting was turned on at 0800 h and off at 2000 h. A 5-day-old female parasitoid female was introduced into a petri dish containing 20 3rd-instar host larvae. Every 4 hours, for the first 12 h of a 24 h day, host larvae were replaced with 20 more 3rd-instar larvae. The numbers of hosts killed and parasitized were counted for each time period.

D. intermedius-induced host mortality and parasitization were highest between 0800 and 1200 h. There was an almost complete absence of parasitism and parasitoid-induced host mortality in the absence of light. The data obtained in this experiment could be utilized in determining, for example, when to spray during the day to produce the least effect on parasitoid densities.

Whether D. intermedius preferred 3rd-instar larvae or 2nd-instar larvae for oviposition was also determined (Chapter VI). An equal number of 2nd- and 3rd-instar host larvae were made available to females singly confined to petri dishes. Significantly more 3rd-instar larvae were parasitized and killed than were 2nd-instar larvae.

Experiments done to determine rates of parasitism and parasitoid-induced host mortality, as functions of host and parasitoid densities, are reported in Chapter VII. Female D. intermedius, along with tomato plants containing 3rd-instar leafminer larvae, were confined to cages in a controlled environment room. The temperature in the room was maintained within the 25-27 C range. Each cage contained 1, 2, 3, 4, or 5 4-day-old female parasitoids. The density of leafminer larvae was altered by exposing clean tomato plants to different densities of leafminer adults for different time intervals. At the end of 12 h of exposure to parasitoids, plants were removed, leaf area was measured, and the numbers of hosts parasitized and killed were recorded.

The data obtained from the experiments were utilized to obtain estimates of parameters permitting description of the relationship between the rate of parasitism and the densities of L. trifolii and D. intermedius by the equation:

$$Y = Kp.e_2(1 - \exp(-e_1/Kh) \quad (r^2 = .79) \quad (T = 25\text{-}27C) \qquad (4)$$

where Y, the parasitism rate, is the number of hosts parasitized per day. In (4), Kp, with a value of 7.3908, is a constant with the unit number of hosts parasitized/parasitoid-day. Densities e_2 and e_1 are, respectively, parasitoids/cage and leafminers/

leaf area (cm^2) and Kh, another constant, is 0.0144 leafminer hosts/leaf area.

Results of the experiments also were utilized to formulate the similar but parametrically different equation (5) below that expresses parasitoid-induced host mortality as a function of host and parasitoid densities at 25-27C.

$$Z = Cp.a_2(1 - \exp(-a_1/Ch) \quad (r^2 = .78) \quad (T = 25\text{-}27) \qquad (5)$$

where Z, the parasitoid-induced host mortality rate, is the number of hosts killed per day. With a value of 9.2064, Cp is a constant with the units number of hosts killed/parasitoid-day and Ch is 0.0165 leafminer hosts/leaf area.

The effect of multiple oviposition on survival of progeny is important in estimating the parasitoid density in the following generation. To study this effect, parasitoid eggs were kept at 4 different densities on host larvae in the experiment reported in Chapter VIII. An average 0.8, 1.1, 1.35 and 0.98 eggs became adults when 1, 2, 3, and 4 eggs, respectively, were kept on each host larva.

The results of all experiments reported in this dissertation are summarized in Chapter IX. In this final chapter, I have also hypothesized that, Ke, the number of parasitoid eggs reaching the adult stage/100 host larvae killed may be described by the equation:

$$Ke = 93 - 800a_1 \qquad (6).$$

In (6), n_1 is the number of leafminers/leaf area (sq cm). The relationship would be true at 25-27 C temperature range only since survivorship of eggs to adult stage was not reported at other temperatures. This equation was obtained from the observed distribution of parasitoid eggs densities on host larvae at different host densities as reported in Chapter VII, and the observed survival rates of different densities of parasitoid eggs on host larvae as reported in Chapter VIII. Although it is not a substitute for a comprehensive leafminer-parasitoid model which has provisions for stage specific mortality, Ke provides a crude estimate of the number of parasitoids expected in the next generation. This could be a useful tool in the field if it is necessary to obtain a quick estimate of the density of parasitoids to be expected in the next generation.

In addition to summarizing the results and suggesting the utility of Ke, I have also suggested that the classical biological approach should not be neglected. Exploration of other regions for leafminer parasitoids not found in Florida, and subsequent importation and establishment of these in Florida should also be seriously considered in the tomato IPM program.

CHAPTER II
LITERATURE REVIEW

Tomato Production in Florida

Importance

In monetary terms, the tomato is the most important vegetable crop grown in Florida (Cantliffe 1985). Total value of the crop increased from $122.3 million in the 1973/74 season to $390.6 million in the 1982/83 season (Van Sickle and Belibasis 1985). Tomato acreage has increased from 31,500 acres in the 1974/75 season to 47,400 acres in the 1983/84 season. Manatee and Hillsborough counties and adjacent areas accounted for 17,500 harvested acres in the 1983/84 season while Dade county harvested 12,800 acres in the same season and Collier and Hendry counties harvested 9,375 acres. These three regions accounted for 40,075 acres of the 47,400 total acres harvested in Florida (Van Sickle and Belibasis 1985). The yield of tomatoes has increased from an average 796 25-pound boxes per acre in the 1973/74 season to an average 1,250 boxes in the 1981/82 season (Van Sickle and Belibasis 1985).

An important aspect of tomato production in Southern Florida is the perceived competition from West Mexico producers for the U.S. domestic market. Both regions supply a large part of the Eastern U.S. winter demand for fresh tomatoes. Van Sickle and Belibasis (1985) have shown that Florida's share of the tomato market has increased over the past 10 years, however. The widespread use of hybrid varieties such as 'FTE-12', 'Duke' and 'Sunny' has contributed to Florida's competative edge over West Mexico, according to these authors. These hybrids have higher yields, firmer fruits and concentrated production compared to the traditional varieties. Fields are now picked only 2 or 3 times, whereas the previous practice was to pick as many as 5 times. In addition, the cost of marketing and shipping Florida tomatoes is less than that for Mexican tomatoes (Van Sickle and Belibasis 1985).

The competitive edge has also been sustained by keeping down the costs of pest control. Twice weekly sprays just to control leafminers was the recommendation to growers by the University of Florida's Institute of Food and Agricultural Sciences (IFAS) in the 1960's (Brogdon et al. 1970). Spray applications by a typical grower for control of all pests were reduced to 14 per season by 1980 (Prevatt, personal communication). The costs (in 1978/1979 prices) of pest control ranged from $228.79 to $438.20 per acre in 1978/1979 season (Brooke 1980). In 1984/85, these costs (in 1984/1985 prices) ranged from $453.43 to $501.96 per acre (Van Sickle and Belibasis 1985).

Production Methods Relevant to Pest Management

There are two tomato growing seasons a year in the Manatee-Hillsborough area of Florida. The 110-day fall season starts in late August and ends in December. The 120-day winter season lasts from January to April. In the Dade, Collier and Hendry counties, tomatoes are grown once a year in a growing season extending from approximately November to February. In northern regions of the state, tomatoes are grown during the spring months. Pest management decisions are made throughout the growing season These decisions are discussed below.

Land selection. Most growers use the same field only in alternate or every fourth season for growing tomato. Some growers avoid using fields with a previous history of consistently bad yields attributable to soil pathogens or nematodes (personal communications).

Land preparation. Rotovating, forming raised beds, preparing irrigation and drainage ditches, fertilizing, fumigating and covering with strip- or full-bed plastic mulch are the cultural practices commonly employed in preparing the land for planting. The soil pH should ideally be maintained in the 6.0 to 6.5 range (Hochmuth 1985). Crop losses due to Fusarium wilt (*Fusarium oxysporum* f. sp. *lycopersici* (Saccardo) Snyder and Hansen races 1, 2, and 3), Fusarium crown rot (*F. oxysporum* f. sp. *radicis-lycopersici* Jarvis & Shoemaker), southern blight (*Sclerotium rolfsii* Saccardo), and and many nematode-incited diseases can be reduced by adjusting the pH to within the 6.5 to 7.5 range (Jones and Overman 1985).

Other soil pathogens are not easily managed by simply regulating the soil pH. These organisms include Verticillium wilt (*Verticillium albo-atrum* Reinke and Berthold races 1 and 2), the damping-off disease caused by *Rhizoctonia solani* Kuhn and *Pythium* spp., Pyrenochaeta brown-rot (*Pyrenochaeta lycopersici* Schneider and

Gerlach), and bacterial wilt (*Pseudomonas solanacearum* E. F. Smith). These organisms are controlled with soil fumigants (Jones and Overman 1985). Hochmuth (1985) recommends that at least 50% of the nitrogen should be in the nitrate form. Blossom-end rot and soil conditions favorable to fusarium wilt can occur as a result of reduced calcium uptake if much of the nitrogen is in the ammoniacal form. He also points out that some pesticides contain elements that are essential micro-nutrients for the tomato. These micro-nutrients should not be given separately if previous soil analyses indicated that they were lacking and if pesticides containing the micronutrients are to be used. Toxicity could occur as a result of build up of some elements. Excess copper could induce iron deficiency, for example.

Tomato yields can be increased greatly by reducing the diseases caused by soil-borne pathogens by using other methods in addition to proper liming and fertilizing regimens. This involves the use of grower-imposed quarantines, exclusion of infected materials, removal and incineration of crop residues, the use of resistant cultivars, and soil fumigation.

Resistant cultivars. 'Sunny', 'Duke', 'FTE 12', 'Cayslip', and 'Floradade' tomato cultivars accounted for 96% of the total acreage in Florida in the 1984/85 season (Hawkins 1985). Most cultivars in current use in Florida are resistant to race 1 verticillium wilt but not to race 2 (Jones and Overman 1985). They are also resistant to *F. oxysporum* f. sp. *lycopersici* races 1 and 2 and to gray leaf spot (*Stemphylium solani* Weber) (Maynard 1986). Scott (1985) has shown true resistance to Fusarium wilt race 3 in LA716 (*Lycopersicon pennellii* (Correll)D'Arcy) accession. Advanced testing of lines resistant to bacterial spot (*Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye), bacterial wilt (*Pseudomonas solanacearum* E. F. Smith) or fusarium crown-rot should occur in the next two years (Scott 1985).

Soil fumigation. It is essential to use broad-spectrum fumigants even when all the other tactics mentioned above are used to control the soil-borne pathogens. The fumigants include methylbromide + chloropicrin, chloropicrin + nematicides, and methylisothiocyanate + nematicides (Jones and Overman 1985).

Weed control. Nightshade (*Solanum americanum* Mill.) is the most important weed in southwest Florida (Gilreath 1985). It belongs to the family Solanaceae as does the tomato. Because of the close genetic relationship between the two plant species, tomato would likely be injured if herbicides were used to control nightshade.

Herbicides can be used to control nightshade if the tomato is grown on mulched, seepage irrigated beds and the spray is directed to the row middle so that it does not contact the tomato plant (Gilreath 1985). Gilreath (1985) found that paraquat (Paraquat ^{R}), metribuzin (Sencor^R /Lexone^R), and other labeled herbicides will control nightshade if applied to nightshade in the 2 to 4 true leaf stage of development. Older plants and those hardened by cold or other factors would not be adequately controlled by labeled hebicides. Gilreath (1985) has evaluated several new currently unregistered herbicides for their efficacy against nightshade and other weeds in tomato. He found that a combination of oxyfluorfen (Goal^{R}) and fluazifop (Fusilade 2000^{R}) provided the best control of many weeds, including nightshade and grasses, and that there was a rapid kill of emerged weeds. It is his hope that Goal^{R} will be registered for use in mulched tomato middle in the next two years.

Other weeds of tomato include the nutsedge (*Cyperus* spp.), ragweed (*Ambrosia artemisiifolia* L.), *Medicago* spp., common beggar-tick (*Bidens pilosa* L.), and downy ground cherry *Physalis pubescens* L.). Almost all weeds other than nightshade are easily controlled by currently registered herbicides. Nutsedge is controlled by methylbromide, for example (Dunn 1985).

Foliar disease management. Regular maneb/mancozeb and copper applications are made to control bacterial infections. They have to be used carefully. Certain copper and mancozeb combinations may lead to higher incidence of target spot (*Corynespora cassiicola* (Berk. & Curt)), than the use of chlorothalonil (Jones and Jones 1984). Conover and Gerhold (1981) showed that maneb or mancozeb alone were more effective than a combination of basic copper sulfate with either maneb or mancozeb in controlling late blight (*Phytophthora infestans* (Montagne) de Bary) and gray leaf spot. Metalaxyl, which is now registered for use on tomato, gives excellent control of the tomato late blight, and related fungi (Pohronezny 1985). Samoucha and Cohen (1984) have shown a high degree of cross-resistance to other compounds by fungus biotypes that have resistance to metalaxyl, however.

A weather-based system, BLITECAST, predicts outbreaks of late blight and is used in many parts of the country. It has not been very useful under Florida conditions, however. First outbreaks of late blight occur much later than predicted by BLITECAST (Pohronezny 1985).

Insect pest management. The tomato is damaged by direct and indirect insect pests. Direct pests attack the marketed product, the fruit. The armyworms (*Spodoptera eridania* (Cramer), *S. exigua* Hubner), and *S. dolichos* (F.)), the tomato pinworm *Keiferia lycopersicella* (Walsingham)), the tomato fruitworm (*Heliothis zea* (Boddie)), the tobacco budworm (*H. virescens* (F.)), and the southern green stink bug (*Nezara viridula* (L.)) are some of the direct insect pests of tomato.

Indirect insect pests of tomato include leafminers as well as most of the pests listed above when they damage plant parts other than the fruit. Defoliation could result in reduced photosynthetic activity and reduced fruit size. The sun may scorch fruit on the vine if leaf shade is removed by defoliation (Musgrave et al. 1975). Pathogens may exploit damaged parts for invasion of the plant. *Alternaria alternata* (Fries) Keissler, which is weakly parasitic, and *Xanthomonas campestris* pv. *vesicatoria* enter leafmines to invade the tomato (Keularts 1980).

Chemical control. Several effective insecticides are available and in current use by growers (Johnson 1985). Permethrin (Ambush^{R}), methomyl (Lannate^R), endosulfan (Thiodan^R), and methamidophos (Monitor^R) are some of the popular insecticides for control of tomato insect pests. Avermectin (Avid^R) and cyromazine (Trigard^R) are new insecticides that are effective against leafminers (Schuster and Everett 1983), but they are currently not registered for use against leafminers on tomato in Florida. The effect of insecticides on leafminers and their natural enemies is described in detail in the section on leafminer control in this chapter.

Integrated pest management. There are essentially two types of strategies for insect management available to growers on tomato. Some growers treat their crops when needed. Other growers spray the crop on a regular basis whether they know pests are present in the field or not. Both strategists employ resistant cultivars, intensive pre-plant treatment of soil with nutrients and multi-purpose fumigation, hebicides and other practices such as staking and mulching.

Growers who treat their crops for insects only when needed, make their decisions on recommendations from professional scouting consultants or use their own judgement. The employment of professional scouts is now widespread (Pohronezny 1985).

Integrated Pest Management (IPM) programs were initiated in the Homestead region in 1976 (Pohronezny and Waddill 1978) and, with modifications, in the Manatee-Ruskin area in 1978 (Schuster et al. 1980). Funding for the programs was from state and federal sources but scouts were encouraged to form private firms and solicit contracts from the growers. There are now at least two tomato IPM consultant companies in the Manatee-Ruskin area, and one in the Homestead region.

Sampling methods remain very similar to those initially developed by Pohronezny and Waddill (1978). Scouts in both areas spend most of their time in the field sampling leafminers and pinworms. All other scouting activity is secondary in that observations of other pests are made at the same sampling stations and while walking from one station to the next. Schuster et al. (1980) described the procedure, technique and leafminer thresholds for the Manatee-Ruskin area. Each field is scouted twice weekly throughout the growing season. More stations are allocated to field boundaries than to the middle of a field, as pinworm and leafminer populations seem to be distributed in clumps, with higher densities of these insects being found near boundaries. There is one sampling station for every 2.5 acres of a field. Plants are sampled for leafminers, pinworms, and other pests.

Live leafminer larvae are now counted instead of the earlier method of counting total mines in deciding whether or not leafminers have reached a population level that required chemical treatment. In considering only live larvae and excluding larvae killed by parasitoids, the role of natural enemies in regulating leafminer populations is recognized (Pohronezny et al. 1984).

The threshold for treating lepidopteran pests has been altered from 1 larva/field to 1 egg/field after fruiting (Schuster et al. 1980). Pena (1983) revised the tomato pinworm threshold to 0.67

larva/plant or 0.83 foliar injury/plant. To save time on the laborious task of counting mines, Schuster and Beck (1983) established a visual rating system for assessing total leafmines.

Liriomyza trifolii (Burgess)

Description

Adult *L. trifolii* are 1.3 mm long. Their wing length is 1.5 mm (Burgess 1880). A full description of a neotypic male specimen reared from alfalfa was given by Spencer (1965) Spencer (1973) also illustrated male genitalia, a character which he uses to differentiate closely related Agromyzidae. *L. sativae* Blanchard is often confused with *L. trifolii*. These species can be readily identified by differences in four features. The curvature of the aedeagus is more pronounced in *L. trifolii* than in *L. sativae*. The *L. trifolii* mesonotum is distinctly grayish-and matte while that of *L. sativae* is shining black. The area of the *L. trifolii* upper orbits and much of the hind margin of the eye is yellow and both vertical bristles are on a yellow background. The upper orbits and much of the hind margin in *L. sativae* is dark and the vertical bristles are on a dark background (Spencer 1981a).

Knodel-Montz and Poe (1982) used scanning electron microscopy to study female adults. They showed that *L. sativae* and *L. trifolii* females can be distinguished by the denticles and the egg guides on the genitalia. The denticles are angular and the egg guide is V-shaped in *L. trifolii*. In *L. sativae*, the denticles are elongate and the egg guide is acutely angled. Zehnder and Trumble (1983) utilized electrophoretic and scanning electron microscopy techniques to separate the two species.

L. trifolii eggs are "oval, creamy or translucent and approximately 0.2 x 0.1 mm (E. A. Mortimer personal communication). The larva, which is initially colorless, darkens to yellow as it matures and the pupa is orange-yellow" (Bartlett and Powell 1981, p. 186).

A distinguishing characteristic of agromyzid larvae is that the anterior pair of spiracles is located dorsally, adjacent to the dorsomeson. The anterior spiracles are laterally located in other cyclorrhaphan larvae (Peterson 1979). The number of bulbs on the posterior is sometimes useful in separating agromyzid species. There are 3 spiracular bulbs in *L. sativae* while 6 bulbs occur in *L. huidobrensis* Blanchard, another closely related species (Spencer 1981a).

The larva has 12 segments (the head, 3 thoracic segments, and 8 abdominal segments). Most, and sometimes all, segments have distinctive minute tubercles in bands that are mainly confined to the segmental boundaries. Muscle scar patterns on the body are also found. The body tends to be cylindrically uniform but the anterior and posterior taper (Allen 1956). Agromyzid larvae have 2 mandibles The mandibles and the rest of the much reduced mouth parts form the cephalopharyngeal skeleton.

Taxonomy

"Article 35 of the International Commission on Zoological Nomenclature states that a name, once placed in homonymy, must be rejected. As a result, the economically important and well-known *Liriomyza trifolii* (Burgess) requires a new name" (Zoebisch 1984, p.5). Zoebisch (1984) has shown from his review of literature on *L. trifolii* taxonomy that the species ought to be renamed since it is a homonym of *Agromyza trifolii* Kaltenbach. *L. trifolii* (Burgess) was first described and named by Burgess (1880) as *Oscinis trifolii*. Coquillett (1898) placed *O. trifolii* in the genus *Agromyza* after having synonymized the species with *Agromyza diminuta*. *O. trifolii* was placed in the genus *Liriomyza* by de Meijere (1925). He was also the first to note the homonymy of *A. trifolii* (Burgess) and *A. trifolii* Kaltenbach. Spencer (1981a) synonymized *L. alliovora* of Frick (1955) and also *L. archboldi* of Frost (1962) with *L. trifolii*.

Distribution

L. trifolii is of nearctic origin. Several authors put its origin in Florida (Spencer 1981b; Parrella and Keil 1984) but the first description of the species made by Burgess (1880) was of a specimen collected from white clover in the District of Columbia. This is important to note as many of the authors who place the origin of the species in Florida also claim that the worldwide spread of the species resulted from the shipping of infested plant material from Florida during the last decade. The species was known to exist in Oregon, California, Indiana as well as Florida and was suspected to occur throughout the U.S. as early as the 1950's (Frick 1959). This is much earlier than the reported spread into the rest of the U.S. from Florida as claimed by Parrella and Keil (1984).

Irrespective of the contention that Florida is the origin of *L. trifolii*, the species is now distributed worldwide. It has been recorded in N. America, S. America, Africa, Europe, and Asia (Table 2-1). A distribution map of *L. trifolii* is available from the Commonwealth Institute of Entomology (CIE) in London, England (CIE 1984).

Host Plant Range

L. trifolii is a polyphagous species (Spencer 1964). The reported host plant range of *L. trifolii* is presented in Table 2-2. Only literature sources published since 1981 have been utilized in the table because there was much confusion about the leafminer species involved prior to Spencer's (1981a) clarification on the differences between *L. trifolii* and *L. sativae*. Hence, the citation of a host plant does not necessarily mean a first record. It is interesting to observe that no author notes more than 100 species as hosts while the total worldwide host plant range is 148 species in 31 families. For example, Stegmaier (1981) does not record watermelon as a host of *L. trifolii* in Florida, while Poe and Montz (1981a, 1982) record that the insect was reared from watermelon in Texas. Pagoonee and Toory (1984) also recovered *L. trifolii* from watermelon in Mauritius.

Table 2-1. Current Known Distribution of *L. trifolii* (Burgess).

Region	Area	Literature source
N. America	California	Poe and Montz 1982
	Florida	"
	Georgia	"
	Hawaii	"
	Indiana	Frick 1959
	Iowa	Stegmaier 1968
	Massachusetts	Vittum 1982
	Mexico	Poe and Montz 1982
	Minnesota	"
	North Carolina	"
	Nova Scotia, Can.	"
	Ohio	"
	Ontario, Can.	"
	Oregon	Frick, 1959
	Pennsylvania	Poe and Montz, 1982
	South Carolina	"
	Texas	"
	Washington	Frick 1959
	Wisconsin	Price 1981
S. America	Colombia	Poe and Montz 1982
Carribean	US Virgin Is.	Poe and Montz 1982
	Bahamas	Spencer and Stegmaier 1973
	Barbados	Spencer 1963
Europe	Denmark	Bartlett and Powell 1981
	Finland	Tuovinen and Aspra 1981
	France	d'Aguillar and Martinez 1979
	Holland	Poe and Montz 1982
	Italy	Arzone 1979
	Malta	Bartlett and Powell 1981
	Spain	"
	Sweden	Nedstam 1981
	U.K.	Anon 1977
	W. Germany	Bartlett and Powell 1981

continued...

Table 2-1 continued.

Region	Area	Literature source
Africa	Canary Is.	Pos and Mentz 1982
	Kenya	de Lima 1979
	Mauritius	Fagoonee and Toory 1983
	Reunion	Vercambre 1980
	Senegal	Spencer 1985
	Tanzania	Spencer 1985
Asia	Israel	Spencer 1985
	Japan	Minkenberg and Lenteren 1986

Table 2-2. Host plant range of *L. trifolii*

Botanical name	Literature source
Acanthaceae	
Thunbergia sp.	Poe and Montz 1982
Amaryllidaceae	
Alstroemeria sp.	Bartlett and Powell 1981
Amaranthaceae	
Amaranthus retroflexus L.	Fagoonee & Toory 1984
A. viridis L.	Zoebisch & Schuster 1984
Celosia sp.	Poe and Montz 1982
Apiaceae	
Apium graveolens	Stegmaier 1981
var. *dulce* (Mill.) Pers.	Stegmaier 1981
Coriandrum sativum L.	Fagoonee & Toory 1984
Daucus carota L.	Broadbent 1982
D. carota var. *sativa* L.	Stegmaier 1981
Hydrocotyle bonariensis Comm. ex Lam.	Fagoonee & Toory 1984
H. umbellata L.	Stegmaier 1981
Pastinaca sativa L.	Powell 1981
Asclepiadaceae	
Asclepias syriaca	Broadbent 1982
Asteraceae	
Ageratum conyzoides L.	Fagoonee & Toory 1984
Ambrosia artemisiifolia L.	Broadbent 1984
Arctium sp.	Broadbent 1982
Aster cordifolius L.	Smith and Broadman 1986
Aster sp.	Stegmaier 1981
Baccharis halimifolia L.	Stegmaier 1981
Bellis perennis L.	Fagoonee & Toory 1984
Bidens alba L.	Zoebisch & Schuster 1984
B. pilosa L.	Stegmaier 1981
Calendula officinalis L.	Powell 1981
Callistephus chinensis (L.) Nees	Stegmaier 1981
Centaurea cyanus L.	Powell 1981
Chrysanthemum leucanthemum	Smith and Broadman 1986
Chrysanthemum X *morifolium* Ramat	Poe and Montz 1981a
Dahlia sp.	Stegmaier 1981
Eclipta prostrata L.	Fagoonee & Toory 1984

continued...

Table 2-2 continued.

Botanical name	Literature source
Erechtites heiracifolia (L.) Raf. ex DC	Stegmaier 1981
Eupatorium coelestinum L.	Stegmaier 1981
E. serotinum Mich X.	Stegmaier 1981
Gaillardia aristata Pursh	Stegmaier 1981
Galinsoga ciliata (Raf.)Blake	Stegmaier 1981
G. quadriradiata Ruiz.& Pav.	Smith and Broadman 1986
Gazania sp.	Bartlett and Powell 1981
Gerbera sp.	Fagoonee & Toory 1984
Gerbera jamesoni Bolus ex Hook	Stegmaier 1981
Gamochaeta pennsylvanica (Willd.)Cabrera (Gnaphalium spathulatum Lam.)	Stegmaier 1981
Helianthus annus L.	Stegmaier 1981
H. bipinnatus Cav.	Smith and Broadman 1986
Hymenopappus scabiosaeus L'Her	Stegmaier 1981
Lactuca canadensis L.	Stegmaier 1981
L. sativa L.	Stegmaier 1981
L. serriola L.	Broadbent 1984
Launaea cornuta (Oliv. & Hiern) Jeffrey	Spencer 1985
Melanthera aspera Mich X	Stegmaier 1981
Mikania scandens (L.) Willd.	Genung 1981
Senecio glabellus Poir.	Stegmaier 1981
S. jacobaea L.	Powell 1981
S. vulgaris L.	Broadbent 1982
Solidago sp.	Broadbent 1982
Sonchus asper (L.) Hill	Stegmaier 1981
S. oleraceus L.	Genung 1981
Synedrella nodiflora (L.) Gaertn.	Stegmaier 1981
Tagetes erecta L.	Stegmaier 1981
T. indica L.	Fagoonee & Toory 1984
Tagetes sp.	Fagoonee & Toory 1984
Taraxacum officinale Weber	Broadbent 1984
Tithonia diversifolia (Hemsl.) Gray	Spencer 1985
Tridax procumbens L.	Stegmaier 1981
Xanthium sp.	Stegmaier 1981
Zinnia sp.	Stegmaier 1981
Balsaminaceae	
Impatiens sp.	Fan and Mentz 1982

continued...

Table 2-2 continued.

Botanical name	Literature source
Boraginaceae	
Cordia myxa L.	Fagoonee & Toory 1984
Brassicaceae	
Brassica campestris var. *rapa* L.	Fagoonee & Toory 1984
B. chinensis L.	Fagoonee & Toory 1984
B. juncea (L.) Czern.	Fagoonee & Toory 1984
B. oleracea var. *botrytis* L.	Fagoonee & Toory 1984
B. oleracea, var. *capitata* L.	Fagoonee & Toory 1984
B. oleracea, var. *gemmifera* L.	Fagoonee & Toory 1984
Capsella bursa-pastoris (L.) Medic.	Powell 1981
Raphanus raphanistrum L.	Broadbent 1982
R. sativus L.	Fagoonee & Toory 1984
Thlaspi arvense L.	Broadbent 1984
Caryophyllaceae	
Dianthus sp.	Poe and Montz 1982
Gypsophila sp.	Poe and Montz 1981a
Stellaria media (L.) Vill	Broadbent 1982
Chenopodiaceae	
Beta vulgaris L.	Stegmaier 1981
Chenopodium album L.	Stegmaier 1981
Spinacea oleracea L.	Stegmaier 1981
Convolvulaceae	
Ipomoea batatas (L.) Lam.	Fagoonee & Toory 1984
Cucurbitaceae	
Citrullus lanatus (Thunb.) Matsumura & Nakai	Poe and Montz 1981a
Cucumis melo L.	Stegmaier 1981
C. sativus L.	Stegmaier 1981
Cucurbita maxima Duchesne	Fagoonee & Toory 1984
C. pepo L.	Stegmaier 1981
Lagenaria siceraria (Molina) Standl.	Fagoonee & Toory 1984
Melothria pendula L.	Genung 1981

continued...

Table 2-2 continued.

Botanical name	Literature source
Euphorbiaceae	
Ricinus communis L.	P. Parkman, personal communication 1986
Fabaceae	
Arachis hypogaea L.	Fagoonee & Toary 1984
Cajanus cajan (L.) Druce	Fagoonee & Toary 1984
Cicer arietinum L.	Fagoonee & Toary 1984
Crotalaria incana L.	Stegmaier 1981
Glycine max (L.) Merr.	Fagoonee & Toary 1984
Lathyrus odoratus L.	Powell 1981
Medicago sativa L.	Stegmaier 1981
M. lupulina L.	Smith and Broadman 1986
Phaseolus aureus Roxb.	Stegmaier 1981
P. coccineus L.	Powell 1981
P. lunatus L. (limensis McFad.?)	Fagoonee & Toary 1984
P. vulgaris L.	Fagoonee & Toary 1984
Pisum sativum L.	Stegmaier 1981
Trifolium repens L.	Stegmaier 1981
Trigonella foenum-graecum L.	Fagoonee & Toary 1984
Vicia faba L.	Fagoonee & Toary 1984
V. angustifolia Reichard	Smith and Broadman 1986
Vigna luteola (Jacq.) Benth.	Genung 1981
V. unguiculata (L.) Walp (repens?)	Fagoonee & Toary 1984
Lamiaceae	
Ajuga reptans Benth.	Spencer 1985
Lamium amplexicaule L.	Broadbent 1984
Salvia splendens Ker-Gawl.	Poe and Montz 1982
Liliaceae	
Allium cepa L. onion	Stegmaier 1981
A. sativum L.	Fagoonee & Toary 1984
A. porrum L.	Fagoonee & Toary 1984
A. schoenoprasum L.	Poe and Montz 1982
Malvaceae	
Abelmoschus esculentus J. C. Wendl.	Stegmaier 1981
Malva moschata L.	Smith and Broadman 1986
M. neglecta Wallr.	Broadbent 1982

continued...

Table 2-2 continued.

Botanical name	Literature source
Oxalidaceae	
Oxalis corniculata L.	Fagoonee & Toory 1984
O. corymbosa DC.	Fagoonee & Toory 1984
O. latifolia HBK.	Fagoonee & Toory 1984
Plantaginaceae	
Plantago lanceolata L.	Broadbent 1984
P. major L.	Broadbent 1984
Polemoniaceae	
Phlox drummondii L.	Fagoonee & Toory 1984
Polygonaceae	
Polygonum convolvulus	Smith and Broadbent 1986
P. persicaria L.	Broadbent 1984
Primulaceae	
Primula sp.	Bartlett and Powell 1981
Ranunculaceae	
Ranunculus repens L.	Powell 1981
R. sp.	Powell 1981
Rosaceae	
Crataegus monogyna Jacq.	Powell 1981
Scrophulariaceae	
Antirrhinum majus L.	Fagoonee & Toory 1984
Linaria canadensis (L.) DC.	Fagoonee & Toory 1984
Solanaceae	
Capsicum sp.	Stegmaier 1981
Lycopersicon esculentum Mill.	Stegmaier 1981
Petunia sp.	Stegmaier 1981
Physalis sp.	Stegmaier 1981
P. pubescens L.	Zoebisch & Schuster 1984
Solanum mauritianum Scop.	Fagoonee & Toory 1984
S. dulcamara L.	Powell 1981
S. indicum L.	Fagoonee & Toory 1984
S. melongena L.	Stegmaier 1981
S. americanum L.	Zoebisch & Schuster 1984
S. nigrum L.	Fagoonee & Toory 1984
S. tuberosum L.	Spencer 1985
Tropaeolaceae	
Tropaeolum majus L.	Powell 1981
T. peregrinum L.	Powell 1981

continued...

Table 2-2 continued.

Botanical name	Literature source
Turneraceae	
Piriqueta caroliniana (Walt.) Urban	Stegmaier 1981
Verbenaceae	
Lantana camara L.	Fagoonee & Toory 1984
Verbena officinalis L.	Fagoonee & Toory 1984
Zygophyllaceae	
Kallstroemia maxima (L.) Hook.& Arn.	Stegmaier 1981
Tribulus terrestris L.	Poe and Mentz 1982

Life History

Eggs are laid singly in the leaf mesophyll by a female inserting her ovipositor through the upper epidermis and creating a depression or 'stipple' which varies in size and shape according to the age of the female (Personal communication Deeg 1980). The larva feeds on the mesophyll, creating a serpentine mine. A trail of fecal material, alternating from one side to another, is deposited in the mine. The mature third-instar larva makes a semi-circular hole in the epidermis and drops to the soil. As with other Agromyzidae, L. trifolii pupates within the cuticle of the last larval instar. Adults emerge from the puparia and can mate on the first day (personal observation). After mating, female begin ovipositing in leaves. Females also feed from punctures made in the leaves. These punctures are larger than oviposition punctures (Zoebisch 1984).

Longevity. Adult lifespan varies with environmental conditions. Temperature and food sources are especially important regulators of longevity. Charlton and Allen (1981) found that at 23.8 C females lived 22.7 days and males lived 13.9 days when the the flies were given honey in addition to the host plant, black-eyed pea. Interestingly, when only honey was provided, males lived an additional 1.9 days, the female lifespan, on the other hand, was shortened by 6.4 days. Supposedly, males also feed from the punctures made by females (Musgrave et al. 1975); however, if this were the case, males would live longer when the host plant was made available in addition to honey.

Leibee (1981a) found that temperature influenced leafminer longevity on celery. The females lived 27.7, 28.3, 16.8, and 14.6 days at 15, 20, 25, and 30 C respectively when a 10% honey solution was provided with celery. Parrella et al. (1983b) showed that female lifespans were 14, 12, and 10 days on chrysanthemum, celery, and tomato, respectively, when honey was also provided (the authors do not report at what temperature the flies were maintained).

Fecundity. Like longevity, the egg laying capacity of leafminers also varies. Once again, temperature, host plant and food supplements influence the fecundity of flies. L. trifolii laid 239.67, 405.67, 288.25, 182.33, and 24.33 eggs at 35, 30, 25, 20, and 15 C, respectively, on celery when the flies were provided with a 10% honey solution (Leibee 1981a). Flies maintained at 23.8 C on black-eyed pea laid 177 eggs (Charlton and Allen 1981). An average 439 eggs was deposited when the flies were given honey also. The mean numbers of viable eggs were 298, 212, and 39 on chrysanthemum, celery and tomato when honey was also given to the flies (Parrella et al. 1983b). The daily oviposition rates peaked on day 1, 2, and 4 at 35, 30, and 25 C, respectively, on celery. Also, oviposition was much reduced at lower temperatures and almost stopped at 15 C (Leibee 1981a). Even though the flies lived much longer at the lower temperatures, they cannot be very damaging to the host plants since fewer eggs are laid.

Provision of additional carbohydrate sources results in increased fecundity. Naturally occurring carbohydrate sources include floral and extra-floral nectars, and aphid and other homopteran honeydew secretions. If such sources were exploited by the flies, their fecundity would be increased. Zoebisch and Schuster (in press) have demonstrated that potato aphid, *Macrosiphum euphorbiae* (Thomas), honeydew on tomato leaflets increased the fecundity and longevity of *L. trifolii* under laboratory conditions.

Developmental times for L. trifolii on some crop plants. Temperature regulates the rate at which *L. trifolii* develop. Host plants also affect developmental times (Table 2-3). It is interesting to note that Leibee (1981a) reports much longer developmental times for the species on celery than other authors report on chrysanthemum, pink bean and tomato. For example, at 15.0 C, larvae on celery mature after 25.8 days while larvae pupate in 12.6 days at 14.8 C on pink bean and in 10.1 days at 15.6 C on tomato. Why development takes much longer on celery is not clear. Celery is not a "bad" host plant for *L. trifolii* since the fly lays comparable numbers of eggs on celery and favored host plants, such as the chrysanthemum (Parrella et al. 1983b).

Mortality. Temperature also influences leafminer mortality. Only 9.4% of the pupae survived at 35 C while almost 10 times as many pupae survived to the adult stage at temperatures ranging from 15 to 30 C (Leibee 1981a). Parrella et al. (1983b) found that at 37.8 C 100% pupae died on White Hurricane cv. chrysanthemum. The host plant also influences mortality of the immature stages. Charlton and Allen (1981) reported that total larval and pupal

Table 2-3. Developmental times for *L. trifolii* immature stages on some crop plants.

Temp C	#days as			Host plant	Literature source
	egg	larva	pupa		
14.8	10.7	12.6	28.0	pink bean	Charlton and Allen 1981
15.0	10.0	25.8	-	celery	Leibee 1981a
15.6	-	10.1	-	tomato	Schuster and Patel 1985
20.0	3.0	8.0	10.6	mum	Charlton and Allen 1981
	4.2	6.7	9.4	pink bean	Charlton and Allen 1981
	4.4	12.0	-	celery	Leibee 1981a
21.1	-	7.1	-	tomato	Schuster and Patel 1985
25.0	2.2	4.7	8.2	mum	Charlton and Allen 1981
	2.9	4.5	8.5	pink bean	Charlton and Allen 1981
	2.3	8.0	-	celery	Leibee 1981a
26.7	-	4.4	-	tomato	Schuster and Patel 1985
30.0	3.8	5.1	6.7	mum	Charlton and Allen 1981
	2.2	3.7	6.8	pink bean	Charlton and Allen 1981
	-	6.8	-	celery	Leibee 1981a
32.2	-	3.5	-	tomato	Schuster and Patel 1985
32.5	5.2	4.5	7.6	mum	Charlton and Allen 1981
	2.0	3.4	6.9	pink bean	Charlton and Allen 1981
	2.0	5.4	-	celery	Leibee 1981a

mortality was 26.9, 26.8, 52.6, and 99.0% on pink bean, black-eyed pea, 'show-off' mum and 'yellow knight' mum, respectively. As humidity is increased, the percentage of pupae becoming adults also increases. More than 60% of the pupae held at any humidity higher than 50% RH survived to become adults.

Circadian behavior. *L. trifolii* exhibits diurnal patterns in many of its primary behavioral phenomena including feeding, oviposition, larval emergence, and adult emergence (Charlton and Allen 1981). Most of these activities occurred primarily in the late morning hours. Most *L. trifolii* larvae emerged from black-eyed pea leaves between 0830 and 1330 h (Charlton and Allen 1981). No larvae exited mines between 1830 and 0630 h. Adult emergence was concentrated between 0930 and 1230 h and no adults emerged from 1530 to 0730 h. Oviposition and feeding continued throughout the daylight hours, but the period of greatest oviposition activity was from 1130 to 1430 h. In this same period, the ratio of punctures/eggs was also at its lowest. Feeding occurred throughout the day, although the number of feeding punctures was the lowest during 0630 to 0830 h and after 2030 h.

Zehnder and Trumble (1984b) used yellow sticky trap cards to monitor adult leafminer activity in tomato. They found that, in 1981, more *L. trifolii* were trapped between 1500 and 2000 h. But in 1982, equal numbers were trapped between 0700-1100 h and 1100-1500 h with fewer adults trapped during 1500-2000 h. It is interesting to note that the period of greatest oviposition activity recorded by Charlton and Allen (1981) coincides with the lower daytime sticky trap counts monitored by Zehnder and Trumble (1982) in 1982. Zehnder and Trumble (1982) contend that the high trap count periods are associated with greater female oviposition activity, arguing that the more active females find the best oviposition sites and increase the time available for oviposition.

Diapause. Attempts by Charlton and Allen (1981) to induce diapause in Californian *L. trifolii* failed. Larew et al. (1986) have shown that *L. trifolii* can overwinter outdoors in Maryland. They suspect that the insect probably diapauses in the pupal stage.

Chemical Control of Leafminers On Tomato

Leibee (1981b) discussed past and contemporary methods of control, the importance of leafminer parasites, and the development of insecticide resistance in *Liriomyza* spp. leafminers on vegetables in Florida. He discussed the effectiveness or non-effectiveness of insecticides used in Florida until 1981 but did not specifically name the leafminer species involved because of the difficulty in verification since voucher specimens were not retained. Several authors have reported on the efficacy of various chemicals against *L. trifolii* on tomato since 1981.

In a detailed study, Schuster and Everett (1983) examined the effects of avermectin, cyromazine, permethrin, fenvalerate (Pydrin ^{R}), and methamidophos on oviposition and survival of *L. trifolii*. Avermectin and cyromazine were effective in controlling the insect on tomato in the field. In the laboratory, avermectin killed *L. trifolii* larvae and pupae and also inhibited oviposition.

Cyromazine had no effect on oviposition. Very few adults emerged from foliage treated with avermectin and none emerged from cyromazine treated foliage because no larvae from this treatment pupated successfully. Methamidophos resulted in 80% of the adults dying within 24 hours after treatment in the laboratory. Permethrin, cyromazine, or avermectin did not induce as high a mortality as did methamidophos. Avermectin is a macrocyclic lactone natural product isolated from the soil microorganism Streptomyces avermitilis n. sp. (Frowe and Dybas 1982). It is effective against insects from several orders and against mites and nematodes. Its mode of action involves inhibition of gamma amino-butyric acid (GABA) mediated neuromuscular junction impulse transmission. Although the chemical has no apparent direct effect on adult mortality, it apparently inhibits the use of the ovipositor. Females are, thus, unable to make oviposition or feeding punctures (Schuster and Everett 1983).

Cyromazine is an insect growth regulator (IGR) with a mode of action that is suspected to be hormonal (Parrella et al. 1983a). Leibee (1985) examined the dosage-response relationship of cyromazine on the development of L. trifolii. Increasing dosage led to higher larval mortality as well as increased numbers of larviform and other abnormally developed pupae. Such pupae failed to become adults. Lindquist and Casey (1985) collected more pupae from methomyl treated greenhouse tomato plants than from cyromazine treated plants. Their study showed that methomyl had no adverse effect on the parasite population density while neither cyromazine nor parasitoid introduction altered the parasitoid population density.

Neem seed extract has been tested for activity against *L. trifolii*. The leaves and seeds of the neem tree, *Azadirachta indica* Juss. have been used in India for hundreds of years as sources of insect repellents and insecticides (Jacobson 1981). It is believed that the principle insecticidal compound, azadirachtin, has IGR properties (Sombold et al. 1982). The chemical is absorbed by roots and translocated to the leaves (Larew et al. 1984, Webb et al. 1984). These authors also report the efficacy of neem seed extract against the puparia when used as a soil drench, suggesting that the active ingredient can be absorbed by the pupae through the puparial cuticle. Webb et al. (1984) have also shown that neem seed extract and the purified azadirachtin are highly active against *L. trifolii*.

Intensive control methods, including the use of several insecticides, are employed whenever outbreaks of *L. trifolii* occur in the greenhouses in England (Powell 1981). The methods include fumigation of empty greenhouses with methyl bromide, twice weekly applications of heptenophos (applied as a high volume, HV, foliar spray), oxamyl applied in granules, permethrin (HV foliar spray), and resmethrin (ultra low volume spray) application.

Biological Control of Leafminers on Tomato.

Poe and Montz (1981b) summarized the parasitoids recovered from *L. trifolii*, *L. sativae*, *L. huidobrensis*, and *L brassicae*. All parasitoids recovered so far were Hymenoptera and included species in the families Braconidae, Cynipidae, Eucoilidae, Eulophidae, and Pteromalidae. Some species, including *Opius dimidiatus* Ashmead (Braconidae), *Ganaspidium* sp. (Eucoilidae), *Halticoptera aenea* (Walker) (Pteromalidae), and the eulophids, *Chrysocharis ainsliei* Crawford, *Closterocerus cinctipennis* (Ashmead), *Diglyphus intermedius*, and *D. begini* (Ashmead) have been recovered from more than one species of leafminers. Schuster (1985) reared the following parasitoids from leafminers infesting tomato in the Bradenton area during 1980 to 1984: *Diglyphus intermedius*, *Diglyphus* sp., *Chrysonotomyia punctiventris* (Crawford), *Diaulinopsis callichroma* Crawford, *Chrysocharis parksi* Crawford, *Opius* sp., *Halticoptera circulus* (Walker), and *Ganaspidium* sp.

Zehnder and Trumble (1984a) indicated that *L. sativae*, *L. trifolii*, and some of their natural enemies could discriminate between host plant species of adjacently grown celery and tomato. *Diglyphus begini*, *D. intermedius*, *Chrysocharis parksi*, *C. ainsliei*, *Halticoptera circulus*, and *Chrysonotomyia punctiventris* were the most abundant parasitoids. *C. parksi* was more numerous on tomato, which was a favored host of *L. sativae*. *D. intermedius* was more active in celery where *L. trifolii* was the predominant leafminer species. The host plant, or the host leafminer species, or both may be involved in observed differential densities of the parasitoid species.

The impact of insecticides on parasitoids has been studied by several workers. Hills and Taylor (1951) and Shorey and Hall (1963) demonstrated that DDT led to an increase in leafminer populations due to a reduction in parasitoid density. The subsequent switch to methoxychlor, dieldrin, endrin, and lindane (Wene 1955) and also to parathion, ethion, and diazinon (Getzin 1960) showed the same results.

Synthetic pyrethroid residues were found to be less toxic to *D. intermedia* than was methomyl when pyrethroids were first introduced to control leafminers (Waddill 1978). Fenvalerate was the least toxic pyrethroid evaluated. A combination of leptophos (Phosvel^{R}) and endosulfan (Thiodan^{R}) sprayed on tomato foliage killed fewer parasitoids than the control (water spray) or any other insecticide tested (Poe et al. 1978). Weekly applications of oxamyl (Vydate ^{R}) on tomato foliage reduced the number of parasitoids reared from excised tomato foliage compared to the water control (Schuster et al. 1979). A single application of oxamyl at rates ranging from 30g AI (active ingredient)/100 l to as high as 119.8g AI/100 l or methamidophos at 89.9g AI/100 l did not reduce parasitoid emergence.

Getzin (1960) recommended integration of chemical and biological control methods by selecting chemicals that would kill leafminers but not the parasitoids. Such chemicals have not been available until recently. Most insecticides used for leafminer control have been broad-spectrum and have induced mortality in parasitoid and leafminer populations.

Schuster and Price (1985) noted that *Opius* sp. and *D. intermedia* were proportionately greater in unsprayed tomatoes than in sprayed tomatoes where *Chrysonotomyia punctiventris* was more abundant. Organophosphates depressed *Diglyphus* spp. while favoring *Chrysonotomyia* spp. in celery (Zehnder and Trumble 1985). The pyrethroid permethrin, on the other hand, seemed to favor *Diglyphus* species. Schuster (1985) noted that the proportions of different parasitoid species varied from season to season. Methomyl and permethrin application reduced population densities of all parasitoids including *D. intermedius* when compared with a water check (Schuster and Price 1985).

Endosulfan in combination with *Bacillus thuringiensis* var *kurstaki* Berliner did not significantly reduce parasitoid numbers after 2 applications while endosulfan alone did reduce parasitoid numbers. *D. intermedius* did not decrease significantly even when endosulfan was applied alone. This suggests a differential activity of endosulfan against the various parasitoids of the leafminers. Such differential activity was also noted with methomyl which was more injurious to *D. intermedius* and *Opius* spp. compared to *Chrysonotomyia punctiventris*.

Methomyl also reduced the percentage of parasitism of leafminers on celery in California as a result of a reduced rate of adult parasitoid survival indicated by the increased number of dead adult parasitoids collected from trays placed under the plants (Trumble 1985). The ratio of leafminers to parasitoids reared was lowest for cyromazine and avermectin treated plants (1.18:1 and 1.41:1 respectively) in 1982.

In 1983, avermectin and a water check had the lowest leafminer to parasitoids ratios (3.80:1 and 4.16:1 respectively). These results suggest that the effects of insecticides could not be readily predicted from one year to the next. Also they do not prove conclusively that there is differential susceptibility of leafminers and parasitoids to cyromazine. Application of avermectin as well as other chemicals altered the composition of the parasitoid complex. Avermectin reduced the numbers of *D. intermedius* reared, but at the same time increased the proportion of *D. begini* in comparison to other treatments. In 1983, no reduction in *D. intermedius* populations was observed in the avermectin treatment. Although Trumble (1985) stated that changing the pesticide shifted the composition of the parasitoid complex, he failed to qualify his conclusions by not emphasizing the differences observed in the composition of the parasitoid complex during the two years in which in the experiments were done.

From a single season of experiments done in 1984, Zehnder and Trumble (1985) reported that out of six insecticides (permethrin, diazinon, naled (Dibrom^{R}), methamidophos, mevinphos (Phosdrin^{R}) and endosulfan) applied to celery, permethrin produced greater parasitoid mortality than any other treatment. The authors also reported that the composition of the parasitoid complex varied with the treatments. Organophosphates favored *C. punctiventris* emergence while permethrin treatment led to recovery of more *Diglyphus* species.

Parasitoid population levels are monitored in a field by recording numbers of live leafminer larvae. Spraying decisions are based on live larvae counts rather than the earlier practice of using total mine counts, which ignored the contribution of parasitoids to regulating leafminer populations (Pohronezny et al. 1984). Most workers (e.g. Trumble and Nakakihara 1983) report parasitoid abundance in fields in terms of % parasitism. This method is faulty because no correlation between % parasitism and actual parasitoid densities in the field is established. Schuster and Beck (unpublished) have formulated a sampling plan for estimating leafminer densities. This plan could be incorporated into a program for correlating % parasitism and parasitoid-host densities in conjunction with measurements made by Marlow et al. (1983) of plant area at different growth stages of the plant.

Utilization of parasitoids is more intense in greenhouse tomato cultivation. Success in regulating leafminer populations with releases of parasitoids into greenhouses has been documented in several parts of the world. Lindquist and Casey (1983) released *Diglyphus* into a greenhouse after an initial population of *L. trifolii* had been established. This treatment gave the same tomato yields as alternative treatments where either cyromazine or methomyl was used as the control agent. Petitt (1984) managed *L. sativae* infestations on greenhouse tomato by vacuuming the plastic mulch, increasing parasitoid populations, particularly of *Opius* sp., and by not using any chemical insecticides in the greenhouse. Lyon (1984) obtained greater success in regulating

L. trifolii populations on greenhouse tomato in France by initially establishing populations of Diglyphus isaea Walker and Dacnusa sibirica Telenga in the greenhouse and the surrounding vegetation rather than waiting to release the parasitoids into infested greenhouses.

Diglyphus intermedius (Girault)

Taxonomic Status, Hosts and Distribution

D. intermedius is one of eighteen species belonging to this genus in the family Eulophidae. The species was described by Girault from one female reared in 1916 from Phytomyza chrysanthemi Kowarz (Gordh and Hendrickson 1979). Hosts of D. intermedius include Agromyza frontella (Rondani), Liriomyza brassicae (Riley) L. sativae, L. trifoliearum Spencer, L. trifolii, Phytomyza atricornis Meigen, P. chrysanthemi, and P. nigra Meigen (Kamm 1977, and Gordh and Hendrickson 1979). Gordh and Hendrickson (1979) consider the species to be nearctic and neotropical in distribution.

Adult External Morphology

The general trend of sexual dimorphism in the subfamily Eulophinae is expressed by the presence of dorsal rami on the funicular segments of the male antennae. This is not evident in Diglyphus, the male of which is distinguished from the female by smaller size and longer marginal fringe on the forewings (Gordh and Hendrickson 1979). The genus Diglyphus has two-segmented funicles and parallel longitudinal grooves on the scutellum. D. intermedius and D. isaea are the only two species in this genus that closely resemble each other. In the female *D. intermedius*, only the basal 0.25-0.35 of the hind tibia is metalic colored with coloration fading along the middle 0.30. In *D. isaea*, the hind tibia is predominantly metallic colored and the metallic color does not fade distally. *D. begini* has pale markings on its antennal scapes the middle and hind tibiae are without apical duskiness and the basal cell of the forewing is sparsely or moderately setose (Gordh and Hendrickson 1979). *D. isaea*, an introduced palearctic species, has not been recorded from Florida.

Parasitoid Abundance in Florida

D. intermedius was at least as numerous as any of the 5 other parasitoids reared during the spring of 1975 from excised tomato foliage from Immokalee (Poe et al. 1978). *D. intermedius* accounted for 46.6% and *Chrysonotomyia formosa* Westwood accounted for 49.7% of all parasitoids reared from excised tomato foliage during the winter and spring of 1975 (Schuster et al. 1979). Schuster and Price (In Press) observed that *D. intermedius* continues to be one of the most common parasitoids found on tomato in Florida.

Biology and Life History

Biological notes on a related species, *D. begini*, were first made by Webster and Parks (1913). Hendrickson and Barth (1978) studied the life history and biology of *D. intermedius* in the laboratory. They reported that *D. intermedius* was a solitary ectoparasitoid of leafminers, although occasionally 2 to 5 parasitoids developed on a single *Liriomyza trifoliearum* larva.

It paralyzed and killed all 3 larval instars, but it usually deposited eggs on 3rd-instars only. Incomplete larval development ocurred when eggs were deposited on 2nd-instar hosts, possibly because of an inadequate food supply. Developmental times were recorded for parasitoids reared at a constant temperature of 25.5 C and 60% RH and a photoperiod of 16L:8D. Hosts were reared on bush snap bean, *Phaseolus vulgaris* cv Bountiful and lima bean *P. limensis* cv Thaxter. As it was difficult to observe parasitoids inside leaf tissue, artificial mines were constructed with small cardboard rings sandwiched between a glass microscope slide and coverslip. The egg, larval, and pupal stages lasted 1, 4, and 6 days, respectively, under the conditions provided.

Patel and Schuster (1983), using a method similar to that of Hendrickson and Barth (1978), measured developmental rates of *D. intermedius* at 15.6, 21.1, 26.7, and 32.3 C constant temperatures. The quadratic regression equation $Y = -0.2028 + 0.0214T - 0.0004T^2$ described the relation found between temperature (T) and the developmental rate/day (Y). At 32.2 C, parasitoid larval mortality averaged 88.3% which was twice the mortality at other temperatures.

The manner of pupation in *D. intermedius* is unusual. The larva changes from light yellow to lime bluish green and constructs 6-8 pillars made from meconium voided at the time of pupation. The pillars extend vertically between the two epidermal layers and are usually laid in pairs along the length of the pupa. It has been suggested that the pillars protect the pupa from being crushed if the leaf dries out and also prevents the pupa from rolling about in its mine. Hendrickson and Barth (1978) noted that a female _D. intermedius_ (N = 6) produced an average 40.2 progeny and lived from 3 to 4 weeks.

Modeling the Leafminer-Parasitoids System

Introduction

Modeling is fast gaining acceptance as a major tool in life system studies, including insect population dynamics research (Ruesink 1975, Huffaker et al. 1976, Barfield and Jones 1979, Shoemaker 1980, Getz and Gutierrez 1982, Stimac 1982). A system can be defined as a composition of interacting objects (Smerage 1980). A model is simply a description of a system and may take many forms. Two factors have contributed to the popularity of the modeling approach. 1) Computers have made it possible, at a rapid pace, to realistically simulate and predict the behavior of real life systems using models. 2) It is becoming increasingly cheaper to simulate rather than establish experiments to develop and test system behavior hypotheses.

The leafminer model of Smerage et al. (1980), for example, can be utilized in predicting leafminer and parasitoid population dynamics much more cheaply and quickly than a field experiment ever could. Models such as that by Smerage et al. also provide a framework in which research towards better understanding of a system can be rationally organized, expressed and analyzed. The model of Smerage et al. has been a motivating factor for much of the research done on leafminers in Florida. It is therefore appropriate to review briefly here this model.

The Smerage et al. Leafminer-Parasitoid Model

This model represents insect population systems in general, although it specifically described the leafminer-parasitoid population system. Figure 2-1 illustrates a conceptual model of the leafminer-parasitoid system. The model pertained to the coupling of within-field egg, larval, pupal and adult populations of leafminers, labeled C_1, C_2, C_3, and C_4, respectively, with the egg, larval, pupal, and adult populations of parasitoids, C_5, C_6, C_7, and C_8, respectively, by the parasitism process H_p. The densities of each class of populations is labeled c_i, where the subscript i, is denoted by the same number as the population. For example leafminer egg population, C_1, has density c_1.

Transformations $H_1,\ldots,H_8$ represent development and physiological mortality. The flow of an individual, from one store to the next, resulted from the individual developing into the next stage. For example, upon completion of the egg stage, a leafminer individual flowed from the leafminer egg store to the leafminer larval store through H_1. Flow into the egg store resulted from oviposition, H_0.

Mortality of an individual in a particular store, for example in the leafminer egg store, resulted in the flow of that individual into a 'sink' for dead individuals. Sinks are denoted by triangular

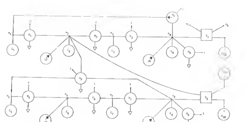

Figure 2-1. Conceptual model of the leafminer-parasitoid system from Sacrage et al. (1980). (see text for explanation)

symbols in Figure 2-1. Temperature dependence of a process is indicated by the terminal labeled T.

Insecticide mortalities affecting larvae and adults were incorporated as extrinsic factors. In Figure 2-1, flow sources, Y_{I2}, Y_{I4}, Y_{I6}, and Y_{I8} remove individuals from their respective age classes at prescribed rates that reflect insecticide induced mortality.

Population density sources s_{e2}, s_{e4}, and s_{8} represent external sources of leafminer larvae, leafminer adults, and parasitoid adults, respectively. Movement of adults between the field is in response to a gradient in an environmental variable. G_4 and G_8 denote the processes that regulate movement of leafminer and parasitoid adults, respectively. Process G_4 may be a function of the quality of vegetation V_F, in the external reservoir, and V_R in the field to which leafminers respond.

Parasitism, Hp, was incorporated as the link between leafminer and parasitoid populations, a process by which attacked hosts were killed and a parasitoid egg was simultaneously oviposited on each host larva. In this model, the rate of parasitism was a function of host and parasitoid densities and environmental variables. The exponential and the rectangular hyperbolic functions represented by equations (7) and (8) are alternative closed-form descriptions of the family of curves for the rate of parasitism when plotted as in Figure 1-1.

$$Y = C_p.Kp.n_2\ (1 - \exp(n_1/Kh)) \qquad (7)$$

$$Y = C_p.Kp.n_2\ (n_1/(n_1 + K1)) \qquad (8)$$

In (7) and (8), Y is the number of hosts parasitized/day and Kp is the specific parasitism rate (hosts/adult-day). In (7) and (8) Kh and Kl represent the critical host density above which Y is nearly independent of host density, n_1. Parasitoid density is denoted by n_1. The capacitance, or the ground area or volume occupied by the parasitoids is represented by C_p.

The mathematical model of the system is not reviewed here. It is sufficient to report here that a mathematical model results in the system being described as a single entity by a set of complex equations systematically obtained from the descriptions of the processes and structure (Smerage 1980). The reader is referred to the chapter on mathematical model in Smerage et al. (1980) if interested in more details or mathematical description of the model.

Several simplifying assumptions were made in formulating the model: 1) the celery crop was a non-limiting host resource for leafminer reproduction and development, 2) all parasitoid species were aggregated into an equivalent single species population, 3) development rates of each species were linear functions of temperature, 4) ovipositing rates were constant and independent of temperature, 5) both populations were uniformly distributed over the field, 6) parasitism was an exponential function of host and parasitoid densities, and 7) movement of both populations was by diffusion or drift.

A combination of hypothetical and preliminary estimates of parameter values obtained from data collected from greenhouse, laboratory, and field studies were utilized to run computer simulations of the Smerage et al. model (Musgrave et al. 1980). These parameters included durations of 40, 40, 90, and 35 degree-days for the leafminer egg, larval, pupal, and adult stages. Corresponding parasitoid durations were 25, 40, 140, and 70 degree-days.

Leafminer sex-ratio was observed to be 1:1 with each female laying 4 eggs/day. The parasitoid sex ratio was not measured but a parasitoid was assumed to lay 1 egg per host, killing 2 hosts/day. Natural mortalities, other than mortality due to parasitization, for the egg, larval, pupal, and adult stages for each egg laid, respectively, were assumed to be 0.4, 0.2, 0.2, and 1.0 for the leafminer, and 0.2, 0.2, 0.1, and 1.0, respectively, for the parasitoid. The critical host density (number of hosts/area), Kh, and the specific parasitism rate (number of hosts parasitized/parasitoid adult-day), Kp, as defined in equation (4) in Chapter 1, were assumed to be 5 larvae/sq m and 2 larvae/adult-day, respectively.

Simulations using several initial conditions provided considerable insight into the influence of various factors on the leafminer-parasitoid population dynamics. Important findings included the observation that sudden outbreaks of leafminers could only be suppressed by the parasitoids 20 to 30 days after the outbreak started. If external reservoirs of leafminers were large, chemical control of leafminers inside the field was ineffective and required frequent and routine applications, and that under these conditions could even be considered wasteful (Musgrave et al. 1980).

More importantly, the work of Smerage et al. (1980) in formulating the leafminer model, and that of Musgrave et al. (1980) in simulating the model has been a significant factor in determining the direction of research on leafminers in Florida. This is especially the case with the work presented in Chapters IV through IX of this dissertation. As with other research currently ongoing in Florida, these chapters describe the work done to obtain better estimates of parameters and descriptions of the processes involved in the leafminer-parasitoid system.

CHAPTER III
PLANT PRODUCTION AND REARING TECHNIQUES FOR *Liriomyza trifolii* (Burgess) AND *Diglyphus intermedius* (Girault)

Introduction

Colonies of *L. trifolii* and *D. intermedius* were maintained to insure that healthy, homogeneous populations of insects were always available. The techniques used for rearing the insects as well as the host plants are described in this chapter. As many as 1000-2000 adults per day of each insect species were produced by using this method.

Several plant species can be used for rearing *L. trifolii* (see section on host plant range in chapter II). Perhaps the fastest and easiest plants to grow are the bean plants, which have been used by several researchers working on *L. trifolii* (e.g. Charlton and Allen 1981). Tomato cultivars 'Walter' and 'Sayelip' were used because the results of the experiments were to be used to understand the leafminer-parasitoid relationship on the tomato.

Host Plant Production

Planting. Tomato seeds were planted in Speedling^R cellular styrofoam trays. In each cell, 4 to 8 seeds were placed 1/2 cm deep in Speedling^R soil mix. The soil pH was maintained between 5.5 and 6.5. Acidic soil mixes were corrected to ideal pH by adding lime or sodium hydroxide. Two trays were planted every Monday, Wednesday, and Friday. As many as 12 trays were planted per week when more plants were needed for the experiments. Seed germination took 3 to 10 days, depending on the temperature.

Trays were watered gently every day, although twice daily watering was required on very hot days. Plants were fertilized twice weekly, 379 g of 20-20-20 (N, P, K) Miller's brand nutrileaf solution was alternated with a solution of 80 g $Mg(NO_3)_2.6H_2O$, 196 g KNO_3 and 336 g of $Ca(NO_3)_2.4H_2O$ in 10 liters of water to give a 500 ppm N, 500 ppm K and 50 ppm Mg solution. The solutions were applied with a Hyponex^R.

Repotting. When the seedlings had reached the first 2-true leaf stage, they were removed and repotted in 6-inch pots. One seedling was planted in each pot if the plant was to be utilized in leafminer-parasitoid density experiments. Four seedlings were planted in each pot for maintaining the insect colonies as well as for rearing insects for other experiments. Potted plants were watered and fertilized the same as the seedlings.

Precautions and care. Chemical pesticides were not applied as long as their use was avoidable. Plants were kept free of insects by good sanitation practices, culling, mechanical control, exploiting natural enemies and the appropriate placing of baits.

Most pest problems were of short duration; they included cockroaches, aphids, Myzus persici (Sulzer), russett mites, Aculops lycopersici (Massee), and on rare occasions, armyworms. Dursban^R baits were placed next to trays of younger seedling plants that were preferred by cockroaches. Russett mite infested plants were discarded and the bench holding infested plants was drenched with Kelthane® (dicofol) and not used for 1 month. Green peach aphids were killed by hand. Heavily infested plants were discarded. On a few occasions, armyworm egg masses were detected on plants inside the screenhouse. Leaves with these egg masses were removed.

Trays and transplants were drenched with a solution of 6.75 g. of Truban® in 8 liters of water. Leafmold became a problem during warm humid conditions. If leafmold was present, Dithane M-45® was sprayed at 18.8 g/l on the plants weekly until the leafmold disappeared. Leaves infested with leafminer larvae were removed.

Rearing *L. trifolii*.

Equipment and procedure. A converted refrigerated truck body housed the leafminer colony. A 12L:12D photoperiod was provided by fluorescent lighting. An air-conditioner and a space heater were utilized to maintain the temperature at 22-32 C. The humidity inside the truck body was uncontrolled and ranged from 40 to 80% RH.

Fifty-200 adult flies were held in a 61 x 61 x 81 cm, organdy cloth-covered, screened, oviposition cage. Four plants were placed in the cage and replaced daily between 0800 and 0900 h with fresh plants. A filter paper smeared with honey was hung from the top of the cage. The honey ensured a large numbers of eggs were laid daily (Charlton and Allen 1981). New flies were added periodically to maintain 50 to 200 flies in the cage.

On removal from the oviposition cage, the plants were shaken to dislodge any flies still on the plants and placed in holding cages. Holding cages were similar to the oviposition cage. Plants were watered daily.

Larvae took 5 days to reach the third-instar. On the sixth day, the plants were removed from the holding cages. Leaves were cut from the plants and placed in Tupperware^{R} (Superseal, 30 x 30 x 12 cm) plastic containers. The containers had screen-covered holes for ventilation. A hardware cloth divider (11 x 11 mm mesh) in the box kept the leaves elevated from the container bottoms. Larvae exiting the leaves dropped to the container bottoms. The bottoms were coated with a layer of Teflon^{R} material to prevent the puparia from sticking to the containers. Leaves were discarded, the hardware screens was removed, and the puparia were gently brushed off the bottoms with a fine camel-hair brush 3 days after the leaves were placed in the containers.

About 50-200 puparia were collected and placed in a 30-g clear plastic creamer cup. A filter paper strip smeared with honey was placed inside the cup. Adults emerged in 4 to 5 days and fed on the honey. A cup containing adult flies was placed inside the oviposition cage and the lid removed so that the adults escaped into the cage.

Leafminers in all stages of development were available daily. It took 14 to 16 days for development of an egg to the adult stage under the conditions prevalent in the rearing facilities .

Precautions and care. All the cages and containers were kept free of standing water to prevent leafminer larvae and puparia from drowning. Plants were watered prior to being placed in the oviposition cage. Since adult longevity is considerably shortened by very high temperatures and the egg laying activity is reduced by temperatures below 17 C, the temperature inside the truck body was monitored with a 7-day hygrothermograph recorder and failures in the air-conditioner and heating unit were corrected as soon as possible after they were noticed. Transfers of exposed plants into holding cages were recorded daily to monitor the age of larvae. Puparia transferred were similarly recorded. Extra leafminer puparia were refrigerated at 5 C and later removed when needed for the leafminer colony on the few occasions that there were not enough adults from the regular colony. Puparia were discarded 1 week after being placed in the refrigerator if they were not needed in the colony.

To maintain vigor of the colony, tomato foliage infested with leafminers was collected from the field approximately every 6 months, and the insects were reared to the adult stage. Fifty to 200 adults were transferred to a new oviposition cage and assimilated into the colony.

Too many ovipositing flies (>200) resulted in too many eggs. Under such overcrowded conditions, plants could be totally defoliated by the developing larvae. The larvae that were able to pupate were smaller. It was, therefore, necessary to ensure that no more than 200 adults were present in the oviposition cage.

Rearing D. intermedius

Equipment and procedure. The parasitoid colony was kept in a separate room with temperature, lighting, and humidity conditions similar to those in the converted refrigerated truck body that housed the leafminer colony.

One or 2 tomato plants containing 5-day-old leafminer larvae were removed daily from the truck body. These plants were placed inside a parasitoid oviposition cage similar to the other cages. Approximately 20 to 100 adults were introduced into the oviposition cage every week. Plants were removed from the cage after 1 day's exposure to the parasitoid adults and replaced with other plants containing 5-day-old leafminer larvae.

Plants with parasitized host larvae were not caged after removal from the oviposition cage to make watering easier. Parasitoid larvae turned bluish-green after 5 to 6 days. At this point, leaflets were stripped from the plants and put in 1-quart ice-cream cartons which were capped by clear plastic bags held to the open top of the cartons by a rubber band.

Adult parasitoids emerged after another 5 to 8 days. A simple aspirator made of flexible rubber tubing and a glass eye-dropper plugged with cotton wool was connected to a small vacuum pump to remove the parasitoid adults from the cartons. Strips of filter paper smeared with honey were placed in 30-g creamer cups and adult parasitoids were put into these cups. Approximately 20 to 100 adults were introduced into the oviposition cage every week. The remaining parasitoids were refrigerated at 5 C. These could be used up to 3 weeks after being placed in the refrigerator. After 3 weeks, the insects were discarded if they were not needed for the colony.

Precautions and care. Plants with more than 400 leafminer larvae were not utilized for the parasitoid colony. It was not easy to maintain these plants because the larvae fed into the leaf petioles causing early leaf drop. Also, it was necessary to water the plants daily since they were under greater stress.

Not all larvae were parasitized. Many dropped onto the cage floor and pupated. Cages were therefore vacuumed every 4 to 5 days to prevent leafminers from becoming adults and ovipositing on the plants.

CHAPTER IV

FECUNDITY AND LONGEVITY OF *Diglyphus intermedius* AND ITS CONTRIBUTION TO HOST MORTALITY

Introduction

Patel and Schuster (1983) had demonstrated that the rates of development of the life stages of *D. intermedius* were functions of temperature. It is logical to hypothetize that, as with other poikilothermic organisms, fecundity and adult longevity of *D. intermedius* may also be functions of temperature. This was recognized by Smerage et al. (1980). In formulating the leafminer model these authors stated that the rates leafminer and parasitoid ovipositions may be functions of temperature. However, for simulation purposes, they assigned constant values for oviposition parameters independent of temperature. They had done this for lack of information on the quantitative description of the relationship between temperature and oviposition rates for leafminers and its parasitoids. Parasitoid fecundity was assumed by these authors to be 2 eggs/parasitoid-day with each host killed yielding 1 parasitoid egg. Parasitoid adults were assumed, for lack of better information, to have a lifespan of 70 degree-days.

It was necessary to obtain better estimates of parameters for parasitoid oviposition and longevity as functions of temperature to represent more accurately the real life situation. Experiments to estimate parameters for parasitoid oviposition and adult female longevity as functions of temperature are reported in this chapter.

In addition, parasitoid-induced host mortality during the adult female lifespan were also measured. To achieve these objectives, experiments were done in a laboratory utilizing *D. intermedius* adults and 3rd-instar *L. trifolii* larvae reared on tomato foliage.

Materials and Methods

Five incubators were utilized to obtain 5 constant temperature conditions. A sixth unit was available as a backup in case a principal unit failed. The temperatures were 15.6, 19.4, 23.3, 27.2, and 31.1 C. Fluorescent and incandescent lighting provided a 12 h photoperiod beginning at 0800 h each day. To record temperature and humidity, a 7-day hygrothermograph recorder was placed on the lower of the 2 shelves in each incubator.

A moistened filter paper was placed in a 150 x 15 mm. clear plastic petri dish. Twenty tomato leaflet pieces, each containing a single 3rd-instar leafminer larva, were arranged in a single layer and placed on the filter paper. A pair of 1-day-old parasitoids were released into each of 4 petri dishes per each of the 5 incubators. The parasitoids were transferred every day between 0800 and 0900 h to new petri dishes containing 20 additional 3rd-instar leafminer larvae. Dead males were replaced with 1-day-old males. The filter paper inside the dish was kept moist to prevent leaflet pieces from drying. No honey or other carbohydrate source was provided.

Live leafminer larvae, empty mines, and dead larvae within mines were counted every day after the parasitoids were transferred to new petri dishes. Hosts containing dead larvae were dissected under a dissecting microscope and larvae with and without parasitoid eggs were counted. The number of eggs laid on each host, as well as parasitoid female longevity, were also recorded.

The experiment was replicated 3 times. Temperatures were assigned randomly to the incubators for the first replicate. Temperature assignment was rotated for 2 additional replicates so that an incubator was not assigned the same temperature again. Data were averaged over replicates prior to analyses with the SAS-GLM procedures (SAS 1982).

Results and Discussion

The mean values for host mortality, parasitoid fecundity, and parasitoid longevity are reported in table 4-1.

Table 4-1. Number of *L. trifolii* larvae killed by and the fecundity and longevity of *D. intermedius* at different constant temperatures. (± 1 SD)

Temp (C)	No. larvae killed	Fecundity	Longevity (days)
15.6	406.6 (168.4)	194.7 (113.3)	43.5 (8.4)
19.4	387.8 (153.0)	221.7 (105.5)	34.4 (6.9)
23.3	281.8 (93.5)	200.2 (107.7)	22.7 (7.7)
27.2	187.8 (55.0)	126.3 (84.4)	16.1 (3.5)
31.1	128.2 (40.5)	67.4 (50.3)	12.4 (3.4)

Host mortality and longevity of *D. intermedius* decreased with an increase in temperature. The mean fecundity of *D. intermedius* increased from 194.7 at 15.6 C to 221.7 at 19.4 C, and then decreased at temperatures greater than 19.4 C. The graphs of regression equations obtained by from mean values for parasitoid fecundity, parasitoid longevity, and parasitoid-induced host mortality for each replicate at each temperature are presented in Figures 4-1, 4-2, and 4-3 respectively.

The low r^2 of *D. intermedius* fecundity, even when a quadratic model was fitted to the observed means, reflect the variations among mean replicate values which in turn reflect variations among individual observations. As there were only 4 observations (only three observations in one case since one female had escaped) in each replicate-temperature combination, the low r^2 value was to be expected. R^2 values of greater than .75 were obtained for *D. intermedius* longevity (Figure 4-2) and parasitoid-induced host mortality (Figure 4-3) when linear regression equations were fitted to the observed means. The results of this experiment can only be utilized to interpret and predict in the 15.6 to 31.1 C temperature range because no measurements were made outside this range.

In the 15.6 to 23.3 C range, the parasitoid's fecundity was higher than that of *L. trifolii* observed by Leibee (1984) on celery. Leibee (1984) reported that *L. trifolii* laid approximately 24 eggs at 15 C and 182 eggs at 20 C when the flies were given a 10% honey solution as an additional food source. The predicted leafminer fecundity ranged from 3 eggs at 15 C to approximately 31 eggs at 30 C when provided with a 5% sugar water solution (Patel 1981). As temperature increased to 31.1 C, *D.*

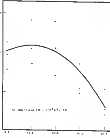

Figure 4-1. Relationship between D. intermedius fecundity, F, and temperature, T. (• = Observation means, n=4)

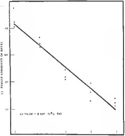

Figure 4-2. Relationship between *D. intermedius* longevity, L, and temperature, T. (• : Observation means, n=4)

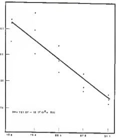

Figure 4-3. Relationship between # hosts killed, Hm, and temperature, T.
(• : Observation means, n=4)

intermedius fecundity declined while that of *L. trifolii* increased.

The maximum parasitoid-induced host mortality and oviposition rates as well as the highest ratio of eggs laid/day: hosts killed/day occurred at 23.3 C (Figure 4-4). The ratio of parasitoid eggs laid/day:hosts killed/day was 0.48, 0.57, 0.71, 0.67, and 0.53 at 15.6, 19.4, 23.3, 27.2, and 31.1 C, respectively. Parasitoid-induced host mortality and oviposition rates at 15.6 C were approximately 24 and 37% less than at 23.3 C. These rates declined by 13.5 and 33.7% when the temperature was increased from 23.3 to 31.1 C. The rate of parasitoid-induced host mortality is apparently less temperature dependent than is the rate of oviposition.

Parasitic hymenoptera have panoistic ovarioles and their eggs develop throughout their adult lifespan. The presence of eggs at all stages of development enables a female to oviposit if hosts are available (Fisher 1971). If all the mature eggs are laid all at once, the female can relatively quickly mature those eggs that are only one stage behind (King and Richards 1969). The rate at which these eggs mature would be expected to depend on temperature, since most developmental phenomena are temperature dependent in poikilothermic organisms.

Parasitoid-induced host mortality, on the other hand, is a behavioral phenomenon. It may be temperature dependent to the extent that the parasitoids may be more active and may take less time to locate and kill hosts at higher temperatures. The actual

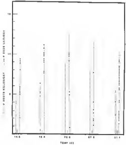

Figure 4-4. Mean daily *D. intermedius*-induced host mortality and *D. intermedius* oviposition at different temperatures.

stinging and paralysis of a host takes only a few seconds, however (Hendrickson and Barth 1978). The arena in which the hosts were placed in the experiment was so small that a parasitoid would not have to spend much time or effort in locating a host. The temperature factor is therefore not likely to have influenced daily host mortality rates as much as it would have affected the daily oviposition rates.

The maximum ovipositions/day of 8.5, 9.5, 13.5, 11.5, and 8.5 eggs/female were reached at 14, 11, 6, 5, and 4 day ages of the parasitoids, respectively, at 15.6, 19.4, 23.3, 27.2, and 31.1 C (Figure 4-5). The maximum parasitoid-induced host mortalities/day were 14 hosts killed at age 7 days, 16 hosts killed at age 12 days, 18.5 hosts killed at age 6 days, 17.5 hosts killed at age 5 days, and 16 hosts killed at age 5 days at 15.6, 19.4, 23.3, 27.2, and 31.1 C, respectively (Figure 4-6).

In comparison to these maximum ovipositions/day and parasitoid-host mortalities/day for *D. intermedius*, *L. trifolii* attained maximum daily ovipositions of 35 to 39 eggs at age 4 days at 25 C, age 2 days at 30 C, and age 1 day at 35 C. The maximum *L. trifolii* ovipositions of 15 eggs in a day occurred at age 5 days at 20 C. Minimal leafminer oviposition occurs at 15 C with a maximum of 2 eggs/female aged 6 days (Leibee 1984). The respective predicted average daily rates for *D. intermedius* at 15, 20, 25, and 30 C are 5.2, 0.7, 0.3, and 0.34 for host mortality and 2.3, 0.4, 0.2, and 0.2 for oviposition for every *L. trifolii* egg laid at the maximum rates as reported by Leibee (1984).

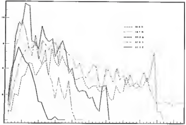

Figure 4-5. Influence of temperature on the number of eggs laid daily by surviving D. intermedius females.

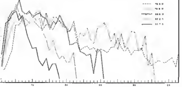

Figure 4-6. Influence of temperature on the number of hosts killed (HK) by surviving D. intermedius females.

With average lifespan host mortality and oviposition rates as high as 5.2 and 2.3 times that of the maximum leafminer oviposition rates at 15 C, it would be expected that *D. intermedius* alone might be adequate for regulating leafminer populations at low temperatures. *D. intermedius* oviposition and host mortality rates can be as low as 0.34 and 0.2 times the maximum *L. trifolii* oviposition rates at temperatures greater than 20 C. *D. intermedius* is at a disadvantage relative to *L. trifolii* with an increase in temperature above 20 C.

Under these circumstances, it might be expected that *L. trifolii* populations may increase under warming conditions. This has been observed in the spring tomato season (Schuster personal communication). The results of the experiments reported here may partially explain why leafminers tend to increase in the spring with a rise in temperature.

CHAPTER V
DIURNAL PATTERN IN OVIPOSITION AND HOST MORTALITY

Introduction

Zehnder and Trumble (1984b) showed that *Liriomyza* spp. leafminers exhibited circadian patterns in flight activity and larval emergence. Flight activity of leafminers peaked between 0700 and 1100 h. Most puparia and emerging larvae were also collected in the same time period.

There have been no studies on the circadian patterns of *Diglyphus intermedius* and patterns of only a few other parasitic Hymenoptera have been studied. Sugimoto and Ishii (1979) noted that daily host mortality from parasitization and host feeding by *Chrysocharis pentheus* (Walker) fluctuated periodically during its life when observed in the laboratory under 24 h light conditions. *C. pentheus* adults parasitized more hosts during the first 6 h and fed on hosts more during the subsequent 3 h in a 24 h period after the parasitoids had been deprived of hosts for 1 day. Nyrop and Simmons (1986) trapped more adults of *Glypta fumiferanae* (Viereck), a parasitoid that attacks the spruce budworm *Choristoneura fumiferana* (Clemens), during the 0800 to 2200 h than in any other time of a day.

If circadian activity patterns of *D. intermedius* were known, sampling and monitoring for the leafminers and *D. intermedius* could be optimized. Also, pesticides could be applied at times that would conserve parasitoids and kill the leafminers.

The experiments reported in this chapter were done to determine the influence of the time of day on parasitoid oviposition and parasitoid-induced host mortality.

Materials and Methods

Five-day-old females were utilized since oviposition and parasitoid-induced host mortality rates peaked on the fifth day at 27.2 C (see chapter IV). Female parasitoids were isolated from the colony upon emergence, paired with day-old males for 1 day, and then placed singly in 150 x 15 mm petri dishes with leaflet pieces containing 30 or more 3rd-instar *L. trifolii* larvae. Fresh host larvae were provided every day. Females were removed at 0730 h on the 5th day and placed in a new petri dish containing host larvae.

For each female tested, 5 petri dishes were prepared. Each petri dish had 20 leaflet pieces with each leaflet piece containing a single 3rd-instar host larva. The petri dishes were held in a refrigerator at 5 C to arrest leafminer development so that no physiological age differences existed between host larvae offered to the parasitoids at different times of the day. The petri dishes were removed from the refrigerator and allowed to equalize to the rearing room temperature for 5 minutes before being utilized for the experiments.

The experiments were done in a rearing room maintained at 25-27 C. Fluorescent lighting inside the room was turned on at

0800 h and off at 2000 h. The parasitoids were transferred to petri dishes with fresh host larvae at 0800 h, 1200 h, 1600 h and 2000 h. Fifteen females, 5 on 1 day, 4 on a 2nd day and 6 on a 3rd day were observed. Killed hosts and parasitoid eggs were counted in the manner described in Chapter IV.

Result and Discussion

The mean number of eggs laid/female in a 24 h period was 14.9 (Table 5-1). This is similar to 11.8 observed for 5-day-old females at 27.2 C in the previous experiments (see Chapter IV). The mean number of hosts killed/female was 14.0 compared to 17.5 as described in chapter IV. The number of eggs laid/female varied from 8 to 23 and the number of hosts killed/female varied from 11 to 24.

Table 5-1. Relationship between time of day and host mortality and oviposition of 5-day-old female O. intermedius at 25-27 C.(± 1 SD).

TIME OF DAY	OVIPOSITION	HOST MORTALITY
0800-1200	10.3 (3.2)	7.9 (1.7)
1200-1600	2.1 (1.9)	2.4 (1.8)
1600-2000	2.4 (1.4)	3.6 (2.2)
2000-0800	0.1 (0.4)	0.1 (0.4)
TOTAL	14.9 (4.7)	14.0 (3.4)

Most of the parasitoid oviposition and parasitoid-induced host mortality activity occurred between 0800 and 1200 h unlike the host killing and ovipositional activity of C. pantheus which preferred to oviposit in the first 6 hours and host-feed during the subsequent 3 hours in a 24-h period (Sugimoto and Ishii 1979).

The parasitoids were not active during the scotophase. Only two of the females were even slightly active at night. None of the other parasitoids killed hosts or laid eggs at night. Parasitoids were not moving and were usually found underneath the leaflet pieces or away from the leaflets when the petri plates were removed for observation at the end of the dark period. In either case, the female parasitoids were at some distance from host larvae when resting. They may, therefore, need vision to search and locate hosts.

During the photophase, there was greater parasitoid oviposition and parasitoid-induced host mortality during the 0800 to 1200 h compared to the 1200 to 1600h and the 1600 to 2000 period. The 5-day-old females had been previously conditioned in the laboratory to have fresh host larvae available to them at the beginning of the day and this may explain why more hosts were killed during the first part of the photophase.

In the field, with most mature larvae emerging by 1100 h (Zehnder and Trumble 1984b), it would be to the advantage of the parasitoid to be most active during the early part of the day. Charlton and Allen (1981) also showed that most mature *L. trifolii* larvae exit from the leaves during the latter part of the morning. Apparently, *D. intermedius* circadian behaviour is linked to the timing of the emergence of mature host larvae from the leaves. This type of behavior would enable the parasitoids to utilize the most mature and, hence, the largest host larvae.

In addition, although presumably equivalent host larvae were offered at 1200 and 1600 h, parasitoid oviposition and parasitoid-induced host mortality activity were much reduced. Thus, laboratory conditioning alone does not fully explain the observed behavior.

If chemical insecticides were to be utilized for leafminer control, it may be best to do so during the period of least parasitoid activity, i.e., during the night hours or in the afternoon or evening. This would allow some adult parasitoids that may be resting away from the plants to escape insecticidal mortality. Spraying at these times may conserve parasitoids but may also be less effective against leafminer adults since their least active period coincides with that of *D. intermedius*. Under such constraints, it may be advisable to use leafminer larvicides. Schuster and Everett (1983) showed that cyromazine (Trigard^{R}) was an effective leafminer larvicide and that Trigard residues on tomato were least lethal to leafminer adults.

CHAPTER VI
HOST STAGE PREFERENCE

Introduction

L. trifolii is attacked by different parasitoids in the field, and it is important to know if any niche division occurs, at least between the major parasitoids, so that competition among them for hosts is understood. Lema and Poe (1979) showed that *Opius* sp., a larval-pupal endoparasitoid and *Chrysonotomyia* sp., a larval endoparasitoid, attacked 72-h-old and 120-h-old *L. sativae* larvae, respectively. The hosts were reared at 20 ± 7.9 C. The *L. trifolii* larval stage lasts about 288 hours at 20 C (Leibee 1984). The larval period of *L. sativae* is probably comparable and hence, 120-h-old larval *L. sativae* are likely to be in their 2nd-instar.

Hendrickson and Barth (1978) showed that *D. intermedius* preferred to oviposit on 3rd-instar rather than 2nd-instar *Liriomyza trifoliearum* Spencer larvae, although it fed on all three instars under laboratory conditions. No parasitoids were reared from 2nd-instar host larvae. Nearly 19% of field collected larvae of the alfalfa blotch leafminer, *Agromyza frontella* (Rondani), were parasitized by *D. intermedius*. This parasitoid preferred 3rd-instar hosts although 23.7% of the parasitized hosts were 2nd-instar larvae. Hendrickson and Barth (1978) attributed the failure of *D. intermedius* in parasitizing 2nd-instar *L. trifoliearum* larvae to the smaller host size.

The preference of a parasitoid for a particular host size is a fairly common phenomenon. *Hyposoter exiguus* (Viereck) laid 2.3 and 1.3 eggs per 24 h in 1st and 2nd instar, respectively, of *Trichoplusia ni* (Hubner) larvae. Oviposition declined for each subsequent instar (Smilowitz and Iwantsch 1975). Successful parasitism by the braconid *Cardiochiles nigriceps* (Viereck) was least in fifth-instar larvae of *Heliothis virescens* (F.) and *H. subflexa* (Guenee) (Lewis and Vinson 1971).

The experiments reported here were done to test if different aged *L. trifolii* larvae are equally acceptable to *D. intermedius* for ovipositional and non-ovipositional purposes.

Materials and Methods

Leafminers and parasitoids were reared as previously described in chapter III. Twenty 96-h-old *L. trifolii* larvae (referred to as young larvae from hereon), and 20 120-h-old larvae (old larvae), in cut tomato leaflet pieces, were arranged in each of 5 150x15 mm petri dishes containing water-moistened filter papers. Five young larvae were alternated with 5 old larvae in each of the radially sectored octants. Two additional plates, one with 20 3rd-instar larvae only, and another with 20 2nd-instar larvae only, were also maintained. A single 5-day-old mated female parasitoid was introduced into each petri dish. The adults were subsequently removed after a period of less than 24 hours and the number of host larvae killed and the number of parasitoid eggs laid were counted. The experiment was replicated 4 times, once on each of 4 days. The exposure period varied for the 4 replicates. The exposure time was the same for each of the petri dishes placed on any particular day. The experiments were done in the rearing room at the prevailing conditions described in chapter V.

Results and Discussion

The results of the experiments are summarized in table 6-1. Significantly more old larvae were killed and parasitized

Table 6-1. Relationship between L. trifolii larva age and mean no. of eggs laid and hosts killed by D. intermedius (± 1SD)

Choice or No choice	#Hosts Killed		#Eggs Laid	
	96h	120h	96h	120h
Choice	3.2 (3.0)	6.0 (3.2)	1.3 (1.7)	5.8 (3.6)
No Choice	10.8 (6.6)	5.0 (5.3)	5.3 (5.1)	5.5 (5.5)

than were young larval hosts when the parasitoids were given a choice (paired t-tests for pooled data, p >.001). Young larvae were as acceptable as old larvae for oviposition and host mortality was the same for larvae of both ages when the parasitoids did not have a choice of different aged hosts.

D. intermedius could utilize synchronous as well as asynchronous host populations under such circumstances. This fact is important to recognize since the application of stage-specific insecticides such as adulticides may tend to synchronize the affected populations for at least a short period.

There may be long term effects on host and parasitoid population densities with synchronous host populations, however. If only small host larvae were present for a long period, parasitoids emerging from small larvae may be smaller. *Trichogramma evanescens* Westwood were smaller when reared on smaller sized *Sitotroga cerealella* (Olivier) host eggs (Salt 1940).

The advantage to *D. intermedium* of attacking larger hosts can be understood if we consider the relationship between hosts and all parasitoids of leafminers. Ectoparasitoids sting their hosts. They cannot rely upon host growth to supply food for their offspring. Endoparasitoids keep their hosts alive and can rely on host growth for their offsprings' growth. Askew (1975) found no early-attacking ectoparasitoids of *Phyllonorycter* spp. leafminers while *Syntomaspis* spp. and *Eurytoma* spp. ectoparasitoids attacked young hosts in oak galls. In oak galls, ectoparasitoids could supplement their diet with gall material whereas there is no provision for phytophagy in leafmines. Askew (1975) suggested that, to a certain extent, the divergence in host selection, with endoparasitoids attacking young leafminers and ectoparasitoids attacking older leafminers, reduced the likelihood of ectoparasitoids attacking a host already containing an endoparasitoid.

The partitioning of hosts between ectoparasitoids and endoparasitoids is not well defined, however. I have reared a *Chrysonotomyia* sp. adult from a field collected *Diglyphus* sp.

pupa. I have also observed *D. intermedius* parasitizing host larvae that have already been parasitized by another individual *D. intermedius*. This suggests that they may not be able to distinguish between parasitized and nonparasitized host larvae or may parasitize hosts even after recognizing the hosts as having been parasitized by others. If this is true, they may just as readily attack endoparasitized host larvae.

In summary, *D. intermedius* kills and oviposits on more 3rd-instar larvae than 2nd-instar larvae if both ages of larvae are equally available to the parasitoid.

CHAPTER VII
IMPACT OF ALTERING HOST AND PARASITOID DENSITY ON DAILY PARASITISM RATE

Introduction

The rate of parasitism in the Musgrave et al. (1980) model was a function of host and parasitoid densities. As mentioned earlier, Figure 1-1 shows the assumed relationship between the rate of parasitism and host and parasitoid densities at a constant temperature. Equations (7) and (8) :

$$Y = C_2.Kp.n_2\ (1 - \exp(n_1/Kh)) \qquad (7)$$

$$Y = C_2.Kp.n_2\ (n_1/(n_1 + K1)) \qquad (8)$$

are alternative closed-form equations generating families of curves, like Figure 1-1, as already mentioned in Chapter II.

In computer simulations of the model, Musgrave et al. (1980) assumed Kh and Kp to be 5 larvae/m^2 and 2 larvae/adult-day. The experiments reported in this chapter were done to obtain a valid description of the rate of parasitism as a function of leafminer and parasitoid densities at a constant temperature. All experiments were done in the laboratory and required the confinement of parasitoids to cages in which leafminer infested plants were kept.

Materials and Methods

Several limitations were encountered in the experimental design. Ideally, observations on parasitoids should be made in a large arena which allows the parasitoids to move naturally in and out of the arena. This would enable the parasitoids to behave naturally and to have random access to hosts, also, the likelihood of encountering the same host again would not be due to confinement to a restricted area. Arena size would certainly be important if the period of observation was large and parasitoids were confined to a small region. Because of the small size of adult parasitoids, it is not possible to monitor parasitoid densities in a large arena with no confinement facilities, however. Nor is it possible to maintain uniformity in leafminer and parasitoid densities between observation plots. It is also not possible to maintain environmental conditions constant.

To overcome these problems, a compromise was made. Female parasitoids were confined in 67 x 67 x 67 cm cages within a controlled environment room for 12 h observation periods. There were several advantages to using cages. *D. intermedius* density per cage was easy to record and manipulate, and other parasitoid species were excluded. As the cages used were relatively small, it was possible to keep them in a controlled environment room and hence at constant temperature and uniform light conditions. One, one-month-old greenhouse grown tomato plant, with approximately 2000 to 3000 sq cm leaf area, was placed in each cage. This amount of leaf area was sufficient to sustain as many as 200 or more leafminer larvae, and a wide range of leafminer densities was possible. With cages, it was possible to alter leafminer densities and maintain uniformity of larval age to a much greater extent than if the experiments were done in the field.

Tomato host plants, cv. Hayslip, used in the experiments were grown and maintained in the greenhouse as described in Chapter III. The plants selected were approximately 30 days post-transplant, 50 to 60 cm tall, had about 10 to 13 leaves, and were just beginning to blossom. Plants of this size just fit into the 67 x 67 x 67 cm cages and allow the maximum amount of leaf area possible on one plant confined in the cage. The plants selected had approximately 2000 to 3000 sq cm leaf area, although on occasion plants were smaller or larger. Plants were moved from one holding area to another with care to minimize the damage to leaves during handling.

After selection, 6 plants were moved to the refrigerated truck body which housed the leafminer colony (see Chapter III). Three tomato plants were exposed to leafminer adults confined in each of two 67 x 67 x 67 cm cages. The number of leafminer adults confined in the oviposition cage was varied from as few as 10 to as many as 50. The exposure period was also varied from as little as 1 minute to 4 hours. It was possible to obtain various leafminer larval densities by manipulating the number of adult flies and the exposure period as just described. After exposure to leafminer adults, the plants were moved to holding cages and maintained in the manner described in Chapter III.

After 5 days, plants containing 3rd-instar larvae were removed at 0800 h and taken to the insectary rearing room for exposure to different densities of parasitoids. Of the 6 plants initially exposed to the flies, 5 plants were selected for exposure to the parasitoids. The plant most different from the others in height or quality or leafminer density was discarded. One plant was placed in each of five 67 x 67 x 67 cm cages.

The parasitoids used in these experiments were collected 4 days earlier on emergence and 40 females and 20 males were confined, 10 females and 5 males to a dish, in 150 X 15 mm petri dishes. Each dish contained 40 to 60 3rd-instar leafminer larvae in tomato leaflets and the larvae were replaced daily. On the 4th day, the parasitoids were isolated singly in size 00 gelatin capsules and sexed, males were discarded. One, 2, 3, 4, or 5 parasitoid females were then released into each of the 5 cages holding the plants. After 12 h plants were removed from the cages, shaken to dislodge parasitoids and transferred to the laboratory adjoining the rearing room at 2000 h.

Plant height, age, number of leaves and leaflets per plant were counted. A Licor^{R} leaf area meter was utilized to record the total leaf area, the area of leaflets containing mines, and the area of leaflets containing parasitized mines. A record was kept of the number of empty, live and parasitized mines in each of 3 leaf categories. Leaves were classified as old (usually the 1st 3 leaves which showed signs of yellowing), fully expanded leaves (the majority of the leaves) and unexpanded leaves (usually the top 3 to leaves although occasionally there may have been several more in a small, tight bundle at the plant apex). Mines containing paralyzed larvae were dissected and the number of eggs laid on each larva was recorded.

The experiment was repeated several times. The assignment of parasitoids to the cages was rotated so that the same cage had the same parasitoid density every 5th time. Because the plants varied in leaf area, and leafminer oviposition could not be made uniform on each plant, it was not possible to regulate leafminer density as freely as parasitoid density. The number of mines on each plant, and hence in each cage, could have been kept the same by destroying some larvae on each plant. However, this would not have been appropriate for 2 reasons. Parasitoids searching a greater leaf area with the same number of mines/cage would take longer than for the same number of mines on a smaller leaf area. Also, destroying leafminers may elicit its own response from the parasitoids if the parasitoids cue in to host plant damage in locating leafminers.

The SAS NLIN pocedure (SAS 1982) was utilized to decribe the relationships between leafminer density and rate of parasitism at different parasitoid densities. The same procedure was also utilized to describe the relationship between leafminer density and parasitoid-induced host mortality at different parasitoid densities. Chi square (X^2) tests were done to determine if there was any effect of altering either leafminer or parasitoid density on the numbers of parasitoid eggs on paralyzed host larvae.

Results and Discussion

Two rate of parasitism models, the rectangular hyperbola and the negative exponential equations proposed earlier by Smerage et

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al. (1908), fit equally well the observed values of rates of parasitism when plotted against leafminer densities in the 0.00-0.06 larvae/sq cm range. The exponential equation obtained using the SAS nonlinear regression techniques was

$$Y = Kp.a_2.(1 - \exp(-a_1/Kh)) \quad (r^2 = .79)\ (T = 25\text{-}27\ C) \quad (4)$$

where Y, the rate of parasitism, is the number of hosts parasitized/day. With a value of 7.3908, Kp is a constant with the units, number of hosts parasitized/parasitoid-day. Densities, a_2 and a_1 are, respectively, parasitoids/cage and leafminer larvae/leaf area (cm^2). Another constant, Kh, is leafminer hosts/leaf area (cm^2).

Results of the experiments also were utilized to formulate the similar but parametrically different equation (5) below expressing parasitoid-induced host mortality as a function of host and parasitoid densities at 25-27 C:

$$Z = Cp.a_2(1 - \exp(-a_1/Ch)) \quad (r^2 = .78)\ (T = 25\text{-}27\ C) \quad (5)$$

where Z, the parasitoid-induced host mortality rate, is the number of hosts killed/day. With a value of 9.2064, Cp is a constant with the units number of hosts killed/parasitoid-day and Ch is 0.0165 leafminer larvae/leaf area (cm^2).

The predicted relationship between host density, parasitoid density and the rate of parasitism utilizing the negative exponential equation is depicted in Figure 7-1. The relationship between rate of parasitoid-induced host mortality and host and

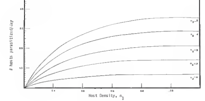

Figure 7-1. Relationship between host density, n_1, and parasitism rate at different parasitoid densities, n_2.

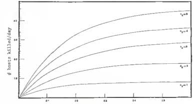

Figure 7-2. Relationship between host density, n_1, and parasitoid-induced host mortality rate at different parasitoid densities, n_2.

parasitoid densities is illustrated by the family of curves in Figure 7-2.

The predicted rate of parasitism at a particular parasitoid density is always lower than the predicted rate of parasitoid-induced host mortality at that parasitoid density. This confirms the previous observation that D. intersedius killed more hosts than it parasitized. However, the proportion of hosts killed that are also parasitized is not the same at all leafminer densities (Table 7-1).

Table 7-1. Proportion of observations with 100% parasitization of killed hosts at different leafminer densities.

Leafminer larvae/ sq cm of leaf area	# of observations with host mortality	# of observations with 100% parasitization of killed hosts
0.00 - 0.0099	38	24
0.01 - 0.0199	19	5
0.02 - 0.0600	33	3

In the 0-0.0099 host larvae/sq cm range, 63% of all observations had a 100% parasitization rate of killed hosts while only 26% and 10% of the observations had 100% parasitization of the killed hosts when the leafminer densities were 0.01-0.0199 and 0.02-0.06 larvae/leaf area (cm^2), respectively.

D. intersedius does not always lay a single egg on each host, as was assumed by Sserage et al. (1980). The observed distribution of parasitoid eggs on host larvae at different leafminer densities is shown in Table 7-2.

Table 7-2. Frequency distribution of killed *L. trifolii* in classes of different *D. intermedius* egg densities.

Leafminer density/sq cm leaf area	# Eggs/killed host larva						Total
	0	1	2	3	4	4+	
0.00 - 0.0099	19	108	60	19	11	16	233
0.01 - 0.0199	42	189	74	31	8	6	350
0.02 - 0.0299	49	163	50	11	10	3	286
0.03 - 0.0399	45	180	46	10	2	2	285
0.04 - 0.0499	43	135	43	9	1	0	231
0.05 - 0.0600	16	40	13	5	0	1	75
0.00 - 0.0600	214	815	286	85	32	28	1460

Strong evidence in favor of a relationship between the number of parasitoid eggs per host larva and host density was shown when a X^2 test was done using the data in Table 7-2 ($X^2 = 67.62$, significant at $p < 0.001$, df = 25). A X^2 test done with observations grouped according to the parasitoid density was not significant at $p < 0.01$ level ($X^2 = 15.6$, df = 20).

It was possible to make some deductions regarding the effect of spatial heterogeneity of host larvae on parasitism rate although this experiment was not designed to specifically test for it. In 68 of 79 observations, the leaflet with the greatest number of mines was encountered by parasitoids as evidenced by the parasitization of at least 1 larva on that leaflet.

In another 4 observations, the parasitoids were similarly attracted to the leaflet with the next highest leafminer density. In the remaining 7 observations, the maximum number of mines on the leaflet was 4. The parasitoids were perhaps equally attracted to leaflets with 4 or fewer larvae at these densities, particularly if many leafminer infested leaflets were close to each other. This was not tested, however, as it would have required determining the area of each leaflet and measuring distance between individual larvae.

A small leaflet with 10 larvae may not have the same attraction to a parasitoid as a large leaflet with the same number of larvae. If the cue, to which the parasitoids responded, is a volatile chemical, there would be greater concentration of the chemical around a smaller leaf area than around a bigger area. There are many instances of parasitoids that have been reported to be strongly attracted by chemicals produced by their hosts (e.g Monteith 1956) or by the damage caused to the plants by the hosts (e.g Vinson 1975).

In this chapter, the rates of parasitism and parasitoid-induced host mortality were shown to be functions of parasitoid and host density. These relationships are represented by equations (4) and (5) for parasitism and parasitoid-induced host mortality, respectively.

CHAPTER VIII
MULTIPLE OVIPOSITION AND ITS INFLUENCE ON PROGENY SURVIVAL RATE

Introduction

It was shown in the experiments reported in the previous chapters that D. *intermedius* does not always lay just a single egg on a host. On one occasion, there were 40 parasitoid eggs on a host. Not all these eggs could possibly survive to the adult stage. Hendrickson and Barth (1978) reported 2 to 5 eggs occasionally developing on a single host larva. I have reared 5 parasitoid adults from a parasitized leafminer larva collected in the field. The number of parasitoid eggs that successfully reach the adult stage may depend on their density on a host larva. The number of surviving progeny of parasitoids may influence the host and parasitoid population densities in subsequent generations.

In this chapter, experiments done to determine the survival of progeny of parasitoids, as influenced by the density of parasitoid eggs on 3rd-instar host larvae, are described.

Materials and Methods

The leafminers and parasitoids used in this experiment were reared in the manner described earlier in Chapter III. Parasitized 3rd-instar leafminer larvae were dissected from mines obtained from the colony and placed in artificial mines constructed in the manner described by Patel and Schuster (1983). Parasitoid eggs, less than 24 h old, were dissected from mines containing parasitized hosts and placed next to the larvae in the artificial mines. One, 2, 3, or 4 parasitoid eggs were placed next to each host larva. A cover slip was placed on the mine and the entire mine was kept in a 100 x 15 mm petri dish containing a water-moistened filter paper. The water-moistened filter paper provided relatively high humidity to prevent the eggs and subsequent stages of the parasitoid from desiccating. The number of host larvae utilized was 12 with 1 egg/larva, 6 with 2 eggs/larva, 4 with 3 eggs/larva, and 3 with 4 eggs/larva. There were 12 eggs at each egg density.

The petri dishes were maintained in the insectary rearing room with temperature, lighting and humidity conditions as previously described in Chapter V. Filter papers in the petri dishes were moistened daily. The petri dishes were kept until no more adult parasitoids emerged from the mines. The experiment was replicated 5 times. The number of parasitoids emerging from each mine was recorded.

SAS ANOVA pocedure (SAS 1982) was utilized to determine if any relationship existed between the initial total number of eggs placed at each egg density and the total number of eggs reaching the adult stage at each density.

Results and Discussion

Results of the experiment are presented in table 8-1. The initial density of eggs/larva is in the 1st column of the table. The mean number of eggs that reached the adult stage, at each egg density, are in the 2nd column. The data in the 2nd column was transferred to obtain the survivorship of eggs to adults/host larva and is shown in the final column.

Table 8-1. Survival of D. intermedius eggs to adult stage when placed at different densities on L. trifolii larvae.

Initial egg density/ host larva (12 eggs at each density)	Mean # eggs surviving to adult stage	Survivorship of eggs/larva
1	9.6a	0.80b
2	6.6b	1.10ab
3	6.0b	1.35a
4	3.0c	0.98ab

Note: means in a column followed by the same letter are not significantly different (Duncan's multiple range test).

At the densities studied, observed survivorship of eggs/larva reached a maximum of 1.35 when 3 eggs were initially placed on a host larva and declined to lower survivorship when the initial egg density was either higher or lower than 3 eggs/larva. Some of the mortality may have resulted from the parasitoids being kept in artificial mines but this would occur at all egg densities.

It would not be appropriate to formulate a regression equation to mathematically describe the relationship between parasitoid survivorship and initial parasitoid egg density based on the limited data reported here if the survivorship of parasitoids is affected by the type of mines. In natural mines, higher survivorship might be expected at all egg densities.

CHAPTER IX
CONCLUSION

Hendrickson and Barth (1978) showed that *D. intermedius* females produced an average 40.2 progeny on *L. trifoliearum* larvae and lived from 3 to 4 weeks. In the experiments described in chapter IV, I have shown that the mean values of *D. intermedius* fecundity, and longevity and of *D. intermedius* induced mortality of *L. trifolii* are temperature dependent. *D. intermedius* fecundity increased from 194.7 eggs at 15.6 C to 221.7 eggs at 19.4 C and then declined to 126.3 eggs at 27.2 C and 67.4 eggs at 31.1 C. The maximum number of host larvae killed was at 15.6 C, the lowest temperature studied. The longevity of female *D. intermedius* was also greatest at 15.6 C, when the females lived for 43.5 days. At 31.1 C, the highest temperature studied, females lived 12.4 days. Equations describing the relationship between temperature and *D. intermedius* fecundity, longevity, and *D. intermedius* induced host mortality are reported in Chapter IV.

D. intermedius fecundity is much higher than leafminer fecundity on tomato reported by Patel (1981) and observed by Leibee (1984) on celery in the 15.6 to 23.3 C range. At temperatures greater than 23.3 C, *D. intermedius* fecundity declined while that of *L. trifolii* on celery and tomato continued to increase. The average daily rates of *D. intermedius*-induced host mortality and *D. intermedius* fecundity on leafminers reared on tomato were 5.2 and 2.3 times, respectively, those of the fecundity of *L.*

trifolii on celery as calculated from Leibee's (1984) data. The peak daily rate of oviposition by *L. trifolii* was between 35 and 39 eggs on celery in the 25 to 30 C temperature range and this peak daily rate was realized in the first 1 to 4 days after the flies emerged (Leibee 1984).

In comparison, peak *D. intermedius* oviposition rate ranged from 8.5 eggs/female-day to 13.5 eggs/female-day and host mortality ranged from 14 to 18.5 larvae/parasitoid female-day in the 19.4 to 31.1 C temperature range. Not only are peak *D. intermedius* oviposition and host mortality rates lower, they also occur later than the peak of leafminer oviposition. Peak rates of *D. intermedius* oviposition and host mortality do not occur until at least the 4th day after the parasitoid adults emerge. At 15 C, *L. trifolii* peak oviposition rate reported by Leibee (1984) was 2 eggs/female-day while a *D. intermedius* female laid 8.5 eggs/day and each female laid a maximum of 14 eggs/day at 15.6 C on leafminers reared on tomato.

If temperature were the only determining factor, *D. intermedius* should be able to limit leafminer populations at low temperatures even on host plants, such as celery, that allow high leafminer population growth rates. At higher temperatures, particularly at 31.1 C, leafminer populations can be expected to increase at a faster rate than *D. intermedius* populations.

D. intermedius was primarily active in killing hosts as well as ovipositing on them during the first 4 h of a 24 h period with 12 h of light and 12 h of dark. There was an almost complete absence of oviposition and host killing activity during the scotophase.

Twice as many 120-h-old *L. trifolii* larvae as 96-h-old larvae were killed by *D. intermedius* when larvae of both ages were made available to *D. intermedius* at the same times and 4 times more eggs were laid on 120-h-old larvae than on 96-h-old larvae. When larvae of either age group were available alone, there was no difference between the two groups in the number of hosts killed or the number of parasitoid eggs laid.

Beddington et al. (1978) proposed that good biological control agents should impose density dependent host mortality. While most researchers report a density dependent relationship between the rate of parasitism and host density (e.g., Hassell 1968), others found alternative relationships between parasitism rate and host and parasitoid densities. Waage (1983) found that among patches of different densities of the host, *Plutella xylostella* (L.), *Diadegma* spp. ichneumonids made the most frequent and longest visits to crop plants with the highest densities of the host insects but the increased total host handling time limited the oviposition rate at high host densities. Parasities/patch as a consequence was density independent. Morrison and Strong (1981) showed that the aggregation of *Cephaloleia consanguinea* Baly (Chrysomelidae) eggs on *Heliconia imbricata* (Kuntze) (Heliconiaceae) leaves improved their chance for escaping attack by eulophids and trichogrammatids to the extent that an inverse relationship existed between the overall probability of parasitism and the number of hosts on each leaf.

I found that the relationship between parasitism/day and the densities of *L. trifolii* and *D. intermedius* can be described by the equation.

$$Y = Kp\ n_2\ (1 - \exp(-n_1/Kh)\quad (r^2 = .79)\ (T = 25\text{-}27\ C)\quad (4)$$

where Y, the parasitism rate, is the number of hosts parasitized/day. With a value of 7.3908, Kp is a constant with the units number of hosts parasitized/parasitoid-day. Densities n_2 and n_1 are, respectively, parasitoids/cage and leafminer larvae/leaf area (sq cm). Another constant, Kh, is 0.0144 leafminer larvae/leaf area. In the equation

$$Z = Cp\ n_2\ (1- \exp(-n_1/Ch)\quad (r^2 = .78)\ (T = 25\text{-}27\ C)\quad (5)$$

Z is the parasitoid-induced host mortality rate, the number of hosts killed/day. The constant Cp is 9.2064 hosts killed/parasitoid-day and Ch is 0.0165 leafminer larvae/leaf area.

These results were obtained with data from laboratory studies involving caged insects and only included parasitoid densities ranging from 1 to 5 females/cage and leafminer larval densities ranging from 0 to 0.06 larvae/sq cm leaf area. I had observed that, as the leafminer density was increased, the number of host larvae that were killed but not subsequently parasitized also increased.

There was a trend toward more _D. intermedius_ eggs/killed _L. trifolii_ larva with decreasing host density. The number of parasitoid eggs/killed host larva increased from 1.14 eggs/larva in the 0.05 to 0.06 leafminer larvae/sq cm leaf area range to 1.82 eggs/larva in the 0 to 0.0099 leafminer larvae/sq cm leaf area range. At low leafminer densities (0 to 0.0099 larvae/sq cm leaf area), approximately 20% of killed host larvae had 3 or more parasitoid eggs. The number of parasitoid eggs/killed host larva did not seem to depend on the density of searching parasitoids, as a X^2 test showed no significant relationship between these variables.

The frequency of survival to adulthood of parasitoid eggs depended on their density on host larvae. An average 0.8, 1.1, 1.35 and 0.98 eggs became adults when 1, 2, 3, and 4 eggs were placed on each host larva respectively. Multiplying the frequency of different egg densities on host larvae, as shown in Table 7-2, with the eggs survivorship shown in Table 8-1 would give an estimate of the number of parasitoid eggs reaching the adult stage at various leafminer larval densities.

For example, with 0 to 0.0099 host larvae/sq cm leaf area, 8 out of every 100 hosts killed had 0 parasitoid eggs, 46 had 1 egg each, 26 had 2 eggs each, 8 had 3 eggs each and the remaining 12 hosts had 4 or more eggs deposited on each of them. If the number of eggs at each egg density is multiplied with survivorship of the eggs at that density, 89 parasitoid adults/initial 100 hosts can be estimated to emerge. The number of parasitoids expected to emerge from 100 host larvae killed at various leafminer densities is shown in Table 9-1.

Table 9-1. Predicted number of parasitoid eggs Ke reaching the adult stage for every 100 hosts killed.

Leafminer density (# larvae/sq cm leaf area)	# Parasitoids reaching the adult stage = Ke
0.00 - 0.0099	89
0.01 - 0.0199	82
0.02 - 0.0299	74
0.03 - 0.0399	64
0.04 - 0.0499	61
0.05 - 0.0800	57

Plotting a graph of estimated K_e values versus mid-range values of the leafminer density classes was used to estimate the linear equation $Ke = 93 - 800n_1$.

It should be noted that leafminer density indirectly determines the number of parasitoids in the next generation. Patel (1981) showed that temperature also influenced the number of parasitoid eggs reaching the adult stage. At 32.2 C, 88.3 % of the eggs failed to reach the adult stage while at 15.5, 21.1, and 26.7 C, about 50 % of the eggs failed to become adults when these eggs were placed on leafminer larvae in artificial mines. Survivorship is expected to be higher in natural mines, but mortality is still to be expected to be dependent on temperature.

Parasitism rate was studied in a rearing room where the temperature was maintained at 25-27 C and using 4-day-old parasitoids only.

These are ideal conditions of temperature and age of parasitoids to estimate maximum rate of parasitism. Parasitoid age and temperature affect the rate of parasitism as described in Chapter IV. Altering temperature and utilizing parasitoid females younger or older than 4 days may reduce the observed parasitism rates. It is, therefore, necessary to establish, through further experimental work, the effects of temperature and parasitoid age on daily parasitism rate as a function of host and parasitoid densities.

As a next step, to better understanding *D. intermedius* and *L. trifolii* population dynamics, sex ratio studies need to be done. A potentially important component is excluded if the effects of host and parasitoid interactions on parasitoid sex ratio are not incorporated into host-parasitoid interaction studies (Hassell and Waage 1984). Sex ratios of the progeny of hymenopterous parasitoids have been shown to be influenced by factors such as host species, host size, host densities, and parasitoid densities (e.g. Flanders 1942, Kochetova 1978, Waage 1982).

I found that virgin *D. intermedius* females produced only male progeny while mated females (paired singly with males for 1 day before testing) produced approximately equal numbers of males and females when each female was provided with 20 3rd-instar host larvae. *D. intermedius* can thus be said to be arrhenotokous and capable of producing male offspring from unfertilized eggs and females from fertilized eggs. Consequently, they can exert considerable control over the sex ratio of their progeny.

D. intermedius is only one of 3 common parasitoids of leafminers on tomato in Florida. Studies similar to those described for *D. intermedius* should also be made for *Opius* spp. and *Chrysonotomyia* spp. parasitoids of leafminers. In addition, field studies should be made to validate or repudiate the results obtained in the laboratory studies. Only then could an IPM program based on host-parasitoid interactions be considered feasible.

The effect of *Opius* spp. parasitoids on leafminer populations and methods for sampling leafminer and parasitoid populations are presently being investigated in Florida by other workers. These studies would complement the current work on *D. intermedius*. Further areas of investigation should include field validation of *D. intermedius* and *Opius* spp. laboratory studies, laboratory and field studies on *Chrysonotomyia* spp., and investigations of the mechanisms and factors influencing dispersal of these insects in crop fields and surrounding areas.

Because of the dynamic nature of interactions between organisms and the ability of organisms to respond to environmental changes through competitive displacement, natural selection, evolution, dispersal and other biological phenomena, results of studies covering a short period of time and utilizing a narrow gene pool may not be universally valid. Leafminers have been shown to be susceptible to many insecticides only to become resistant to them after a period of continued use (see Chapter II). With the current state of IPM on tomato, it is unlikely that the use of chemical pesticides will be eliminated.

The need for continued use of chemical pesticide and the realization that additional studies are required to describe more accurately the host-parasitoid interactions, necessitates consideration of alternative leafminer management strategies. It is possible, that under Florida conditions, leafminer regulation by D. intermedius is ineffective at high temperatures which persist for a long period during the growing season. If this is indeed the case, then exploration of warmer climates for leafminer parasitoids may provide alternative parasitoid species or strains that could be introduced into Florida and could give better leafminer population regulation at higher temperatures.

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BIOGRAPHICAL SKETCH

Kirtikumar Jashbhai Patel was born in Mbale, Uganda, in 1951 and attended Mbale Senior Secondary School during the years 1965 to 1970. In 1972, he obtained a scholarship to study at Balliol College, Oxford University, England. He graduated in 1974 from Oxford with a B.A. Honors in agriculture and forestry sciences.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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